RESEARCH ARTICLE



Anatomical and phylogenetic investigation of the genera Alabastrina Kobelt, 1904, Siretia Pallary, 1926, and Otala Schumacher, 1817 (Stylommatophora, Helicidae)

Jeannette Kneubühler^{1,2}, Rainer Hutterer³, Beat Pfarrer^{1,2}, Eike Neubert^{1,2}

I Naturhistorisches Museum der Burgergemeinde Bern, 3005 Bern, Switzerland 2 Institute of Ecology and Evolution, University of Bern, 3012 Bern, Switzerland 3 Zoologisches Forschungsmuseum Alexander Koenig, 53113 Bonn, Germany

Corresponding author: *Jeannette Kneubühler* (jeannette.kneubuehler@nmbe.ch)

Academic editor: Ton de Winter		Received 4 January 2019 Accepted 1 April 2019 Published 9 May 2019					
http://zoobank.org/4821C74E-C7E8-4866-9BAE-9A03CC46AD16							

Citation: Kneubühler J, Hutterer R, Pfarrer B, Neubert E (2019) Anatomical and phylogenetic investigation of the genera *Alabastrina* Kobelt, 1904, *Siretia* Pallary, 1926, and *Otala* Schumacher, 1817 (Stylommatophora, Helicidae). ZooKeys 843: 1–37. https://doi.org/10.3897/zookeys.843.32867

Abstract

This study presents new insights in the anatomy of genital organs of some large helicid gastropods from northern Africa. The genetic analysis with the markers COI, 16S, H3, and 5.8 S rRNA+ITS2 reveales a high support for *Alabastrina* and *Otala* as separate evolutionary lineages within the Otalini. The position of *Siretia* as another separate lineage within the Otalini is discussed. "*Tingitana minettei decussata*" clusters within the *O. xanthodon* clade and confirms that the genus *Tingitana* can be synonymised with *Otala*. The genus *Alabastrina* differs from all other known genera by possession of a penial appendix. This character state is also found in topotypic *A. tistutensis*. Examination of the twin penial papilla system in *Otala* recovers a reduction of the proximal penial papilla in *O. punctata*. The position of *Helix murcica* as a separate subspecies of *O. lactea* is not supported, and it is here considered to be a synonym of the latter species.

Keywords

Alabastrina, genital anatomy, integrative taxonomy, Morocco, Otala, phylogeny, Siretia, Spain

Introduction

Working with the terrestrial molluscs from northern Africa, students are faced with a confusing situation: an enormous number of species- and genus-level taxa are available to arrange the malacodiversity but for many groups a modern treatment is missing. As a result, this important part of the Palaearctic fauna is still in a chaotic state (Rour et al. 2002). The major problem in the Helicidae is the absence of a stable generic concept that is based on recognisable character states. This can be morphological, anatomical, or genetic data. For this reason, we follow the idea of integrative taxonomy and try to draw conclusions based on a synopsis of these types of traits.

Research on the malacofauna of northern Africa was mainly elaborated by three researchers, Bourguignat (1829–1892), Kobelt (1840–1916), and Pallary (1869–1942), who laid a fundament so strict that it is followed more or less until today. This system was more or less supported by P Hesse (1911) by his anatomical research on some groups of Helicidae. His research was the onset of the valorisation of genital morphology as another source of characters and character states. Amongst others, he investigated species, which are treated also in this publication. Unfortunately, Hesse restricted his research to the outer morphology of the genital organs thus missing the highly informative traits found in the lumen. While in the remaining part of the western Palaearctic, taxonomy of terrestrial snails went through a phase of deep changes, northern Africa was left more or less untouched. This situation is currently changing, and several papers were published in the last years which resulted in new data, for example on the Helicidae (Psonis et al. 2013, Neubert 2014, Neubert and Korábek 2015, Walther et al. 2016, Bouaziz-Yahiatene et al. 2017). Recently, Holyoak and Holyoak (2017) published a major paper on the large group of Otalini G Pfeffer, 1930, which has its centre of radiation in the north-west of Africa. In this paper, the authors went through numerous available names and came up with a radical solution following a lumping approach.

The investigation in this study is mainly based on specimens collected by the second author during his excavation campaigns in north-eastern Morocco (Hutterer et al. 2011a, b. 2014). The taxonomic investigation of terrestrial molluscs was part of an archaeological study of various cave sediments in the Rif region (Mikdad et al. 2000).

This study aims to serve as an addition to the recent studies on helicid phylogeny. Due to the restricted number of taxa available in our study, we here can add only some remarks to the ongoing work on the north African Helicidae. Particular emphasis is laid on filling gaps in the knowledge of the anatomy of the genital organs. It has to be stressed that the investigation of this complex of organs should always include the structure of the internal lumina; they certainly help in identifying autapomorphic character states. In addition, we supply new data on shell and anatomical traits, and present a first genetic approach to some of the genera involved using the following markers: cytochrome c oxidase subunit I (COI), 16S rRNA (16S), histone 3 (H3), and partial sequence of 5.8 S rRNA flanking the internal transcribed spacer 2 (ITS2).

Material and methods

Specimens investigated

The specimens were collected in Morocco and Algeria between 1998 and 2015. Reference specimens from Spain and Portugal could be included. Detailed sampling locations of the investigated specimens are given in Fig. 1 and Table 1. The voucher number and the GenBank accession numbers for the obtained DNA sequences can be found in Table 1. All specimens used in this study are housed in the Natural History Museum Bern, Switzerland.

Abbreviations of institution:

MHNL	Musée de Confluence, Lyon
MNHN	Museum National d'Histoire Naturelle, Paris
NMBE	Naturhistorisches Museum, Bern
SMF	Research Institute Senckenberg, Frankfurt



Figure 1. Sampling locations of the investigated specimens. This map was produced with QGIS (2016, v2.18.12) using the Natural Earth data set.

Species	Locality	Latitude	Longitude	Voucher	GenBank	GenBank	GenBank	GenBank
					accession number COI	accession number 16S	accession number H3	accession number ITS2
Alabastrina alabastrites	Morocco, Montes de Kebdana, Kebdana Mountain/ Rif	35.027N	2.614W	NMBE-549817	MK754458	MK585087	MK728781	MK585111
	Morocco, Rif Jbel Fiztoutine w Hills El Batel	34.938N	3.193W	NMBE-549813	MK754457	MK585086	MK728780	MK585110
	Morocco, Cave Ifri n'Ammar, 20 km SW Berkane	34.782N	3.094W	NMBE-549812	MK754456	MK585085	MK728779	MK585109
	Morocco, Hassi Ouenzga nach Afso/ Oriental	34.796N	3.195W	NMBE-549811	MK754455	MK585084	MK728778	MK585108
	Morocco, Etsedda/ Kebdane	35.195N	3.269W	NMBE-549816	MK754459	MK585088	MK728782	MK585112
Alabastrina tistutensis	Morocco, Rif, Tiztou- tine, village bouaza	34.955N	3.166W	NMBE-555174	MK754469	MK585099	MK728792	MK585123
Allognathus balearicus	Spain, Mallorca, Escorça	39.822N	2.887E	EHUMC-1051	KR705026	KR704986	no data	no data
Arianta arbustorum	Austria, Upper Austria, Höllengebirge Mts	no data	no data	NHM-109000	KF596871	KF596823	KF596915	no data
Helix	Tunisia, Kasserine	35.172N	8.831E	NMBE-540550	MF564162	MF564116	MF564178	no data
melanostoma	France, between Ra- bieux and Saint-Félix- de-Lodez/ Herault	43.663N	3.441E	NMBE-520822	MK754471	MF564115	MF564177	no data
Marmorana muralis	Italy, Rome	41.885N	12.481E	MN-2554	KR705023	KR704983	no data	no data
Massylaea constantina	Algeria, Ighil Bourmi	36.487N	4.061E	NMBE-540545	MF564168	MF564122	MF564185	no data
Massylaea vermiculata	Algeria, Makouda, Tizi Ouzou/ Kabylie	36.791N	4.066E	NMBE-540544	MF564159	MF564112	MF564174	no data
Otala lactea	Spain, Finca de la Concepción, N Málaga	36.760N	4.428W	NMBE-554174	MK754463	MK585093	MK728786	MK585117
	Spain, Punta Entinas, W Almería	36.690N	2.694W	NMBE-554175	MK754464	MK585094	MK728787	MK585118
	Spain, Punta Entinas, W Almería	36.690N	2.694W	NMBE-554176	MK754465	MK585095	MK728788	MK585119
	Portugal, W Almoc- ageme/ Sintra Cascais National Park	38.798N	9.485W	NMBE-553246	MK754460	MK585089	MK728783	MK585113
	Morocco, Hassi Ouen- zga/ Oriental	34.698N	3.256W	NMBE-555171	MK754452	MK585081	MK728775	MK585105
	Morocco, Hassi Ouen- zga/ Oriental	34.698N	3.256W	NMBE-549814	MK754468	MK585098	MK728791	MK585122
	Morocco, West of Aoulouz/ Souss-Massa- Draa	30.709N	8.268W	NMBE-549951	MK754472	MK603015	MK728794	MK602877
	Morocco, Etsedda/ Kebdane	35.195N	3.269W	NMBE-545594	MK754448	MK585077	MK728771	MK585101
Otala punctata	Spain, El Tarajal, W Málaga	36.705N	4.506W	NMBE-554171	MK754462	MK585092	MK728785	MK585116
-	Spain, El Tarajal, W Málaga	36.705N	4.506W	NMBE-554172	MK754467	MK585097	MK728790	MK585121
	Algeria, Makouda, Tizi Ouzou/ Kabylie	36.745N	4.068E	NMBE-534228	MK754466	MK585096	MK728789	MK585120
Otala tingitana	Morocco, Tarzout de Guigou/ Boulmane, NW Boulmane	33.381N	4.778E	NMBE-510549	no data	no data	no data	no data

 Table I. Detailed list of the sampling sites and the GenBank accession numbers of the investigated specimens.

Species	Locality	Latitude	Longitude	Voucher	GenBank accession number COI	GenBank accession number 16S	GenBank accession number H3	GenBank accession number ITS2
Otala xanthodon	Morocco, Kebdana, Moulouya valley S Mechraa Elmalh	34.821N	2.745W	NMBE-555169	MK754450	MK585079	MK728773	MK585103
	Morocco, Kebdana, Moulouya valley S Mechraa Elmalh	34.821N	2.745W	NMBE-555170	MK754451	MK585080	MK728774	MK585104
	Kebdana, Moulouya valley below barrage	34.739N	2.803W	NMBE-549825	MK754453	MK585082	MK728776	MK585106
	Kebdana, Moulouya valley below barrage	34.739N	2.803W	NMBE-549826	MK754454	MK585083	MK728777	MK585107
	Morocco, Montes de Kebdana, Kebdana Mountain/ Rif	35.027N	2.614W	NMBE-549841	MK754473	MK603016	MK728795	MK602878
	Morocco, Montes de Kebdana, Djebel Sebaa Reyal/ Rif	35.030N	2.613W	NMBE-549843	MK754474	MK603017	MK728796	MK602879
	Morocco, Guercif, Oued Melloulon/ Taza al-Hoceima	34.207N	3.414W	NMBE-549820	MK754449	MK585078	MK728772	MK585102
Siretia pallaryi	Morocco, Montes de Kebdana, Kebdana Mountain/ Rif	35.027N	2.614W	NMBE-549815	MK754461	MK585090	MK728784	MK585114
Theba subdentata subdentata	Morocco, West of Aoulouz/ Souss-Massa- Draa	30.709N	8.268W	NMBE-549949	MF564172	MF564126	MF564188	no data
" Tingitana minettei decussata"	Morocco, Montes de Kebdana, Djebel Sebaa Reyal/ Rif	35.030N	2.613W	NMBE-549840	MK754470	MK585100	MK728793	MK585124

Molecular study

For total DNA extraction the Qiagen Blood and Tissue Kit (Qiagen; Hilden, Germany) was used in combination with a QIAcube extraction robot. Ca. 0.5 cm³ of foot tissue was cut from the foot muscle and placed in a mix of 180 µl ATL buffer and 20 µl Proteinase K. It was then incubated for ca. 4 hours at 56 °C in a heater (Labnet, Vortemp 56, witec AG, Littau, Switzerland). For subsequent DNA extraction the QIAcube extraction robot with the Protocol 430 (DNeasy Blood Tissue and Rodent tails Standard) was used. In this study, two mitochondrial markers (COI and 16S) and two nuclear markers (H3 and 5.8 S rRNA+ITS2) were investigated. PCR mixtures consisted of 12.5 µl GoTaq G2 HotStart Green Master Mix (Promega M7423), 8.5 µl ddH,O, 1 µl forward and reverse primer each, and 2 µl DNA template. In Table 2 the used primer pairs for the PCR are listed. Following PCR cycles were used: for COI 2 min at 94 °C, followed by 35 cycles of 1 min at 95 °C, 1 min at 40 °C and 1 min at 72 °C and finally, 5 min at 72 °C; for 16S 5 min at 95 °C, followed by 45 cycles of 30 s at 95 °C, 30 s at 48 °C and 45 s at 72 °C, and finally, 5 min at 72 °C; for H3 3 min at 95 °C, followed 40 cycles of 1 min at 95 °C, 1 min at 42 °C and 1 min at 72 °C, and finally, 10 min at 72 °C, and for 5.8 S rRNA+ITS2 1 min at 96 °C, followed by 45 cycles of 30 s at 94 °C, 30 s at 50 °C and 1 min at 72 °C, and finally, 10 min at 72 °C (SensoQuest Tabcyclet and Techne TC-512,

Gene	Primer	Sequence	Sequence length (bp)	Reference
COI	LCO1490	5'-GGTCAACAAATCATAAAGATATTGG-3'	680	Folmer et al. 1994
	HCO2198	5'-TAAACTTCAGGGTGACCAAAAAATCA-3'		
16S	16S ar	5'-CGC CTG TTT ATC AAA AAC AT-3'	440	Simon et al. 1994
	16S br	5'- CCG GTC TGA ACT CTG ATC AT -3'		
H3	H3AD	5'-ATGGCTCGTACCAAGCAGACVGC-3'	380	Colgan et al. 1998
	H3BD	5'-ATATCCTTRGGCATRATRGTGAC-3'		
ITS2	ITS2ModA	5'-GCTTGCGGAGAATTAATGTGAA-3'	900	Bouaziz-Yahiatene et al.
	ITS2ModB	5'-GGTACCTTGTTCGCTATCGGA-3'		2017

Table 2. Used primer pairs for the two mitochondrial and two nuclear markers.

witec AG, Littau, Switzerland). The purification and sequencing of the PCR product was performed by LGC (LGC Genomics Berlin, Germany). Interpretation of Bootstrap values: 70 to 80 = moderate support; 80 to 90 = well supported; > 90 = high support. Bayesian posterior probabilities: values above 0.95 are significant support.

Phylogenetic analyses

For the phylogenetic analyses sequences obtained from GenBank were included as outgroups: *Arianta arbustorum* (Linnaeus, 1758) (Cadahia et al. 2014), *Marmorana muralis* (OF Müller, 1774), and *Allognathus balearicus* (Rossmässler, 1838) (= *Allognathus hispanicus* (Rossmässler, 1838)) (Neiber and Hausdorf 2015). Additionally, sequences of *Helix melanostoma* Draparnaud, 1801, *Theba subdentata subdentata* (Férussac, 1821), *Massylaea constantina* (E Forbes, 1838) and *Massylaea vermiculata* (OF Müller, 1774) from the study of Bouaziz-Yahiatene et al. 2017 were also included as outgroups. These species were selected to identify the phylogenetic placement of the focal taxa investigated in this study.

For sequence processing and editing the software package Geneious v9.1.8 (Biomatters Ltd) was used. The protein-coding gene fragments of COI and H3 were defined in two data blocks. The first two codon positions were defined as one block and the third codon position as a second block. The non-coding regions from 16S and 5.8 S rRNA+ITS2 were defined as a single data block. Partitionfinder-2.1.1 (Lanfear et al. 2012) was applied for searching optimal evolutionary models for the partitions using the corrected Akaike Information Criterion (cAIC). RAxML plug-in for Geneious (Stamatakis 2006) was implemented for computing ML inference, using Geneious' plug-in with rapid bootstrapping setting, the search for the best scoring ML tree and 1500 bootstrapping replicates. Bayesian Inference (BI) was performed using Mr. Bayes v3.2.6 ×64 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; Altekar et al. 2004) through the HPC cluster from the University of Bern (http://www.id.unibe.ch/hpc). For the concatenated data set, Partitionfinder-2.1.1 was used for finding the optimal evolutionary models for each subset with the model = all function. The Monte Carlo Markov Chain (MCMC) parameter was set as follows: starting with four chains and four separate runs for 20 million generations with a tree sampling frequency of 1000 and a burn in of 25%.

Anatomical and morphological study

Living animals were killed in boiling water and stored for one day in 80% ethanol. The next day, the ethanol was exchanged and the specimens were stored in the fridge at 5 °C until DNA extraction and dissection. Our experience showed that this procedure maintains the soft tissue and is essential for proper anatomical studies, as well as for the conservation of DNA. The dissection of the snail genitalia took place under a stereomicroscope (Leica MZ12) using thin tweezers and scissors. The genitalia were dissected from the body, spread on a wax bedded bowl, and properly pinned with small needles. The total length of the situs was measured using a calliper (Mitutoyo). Proportions between different parts of the genitalia were estimated using the total situs length as a reference. Additionally, the inner structures of the penis and the epiphallus were investigated. Pictures of the situs were taken with a Leica DFC425 microscope camera using an image-processing program (IMS Client V15Q4, Imagic, Switzerland). The empty shells were imaged using a camera (Canon EOS 50D) in a frontal, lateral, apical, and ventral position. The shell height and shell diameter were measured with perpendicular shell axis with the calliper.

Abbreviations used in the anatomical descriptions and figures:

At	atrium	HD	hermaphroditic duct
AG	albumin gland	MG	mucus glands
AS	atrial stimulator	MRP	musculus retractor penis
BC	bursa copulatrix	PA	penial appendix
BCD	diverticulum of the bursa cop-	Pe	penis
	ulatrix	PF	penial flap
D	shell diameter	PP1	proximal penial papilla
DS	dart sac	PP2	distal penial papilla
Ер	epiphallus	PS	penis sheath
Fl	flagellum	Va	vagina
FO	free oviduct	VD	vas deferens
Н	shell height		

Results

Phylogenetic results

The RAxML analysis of the concatenated data set (Fig. 2) recovered the genus *Alabastrina* as sister genus to *Siretia* and *Otala*. This node is supported with a ML support value of 90. The species *A. tistutensis* Galindo, 2018 clusters within the five specimens of *A. alabastrites* (Michaud, 1833). The monophyly of *S. pallaryi* (Kobelt, 1909) and *Otala* (and thus the separation of *S. pallaryi* and *Alabastrina*) is highly supported (bootstrap value of 99). The monophyly of *Otala* is not statistically supported (bootstrap value of 61). Within *Otala* we recovered three major clades, i.e., *O. punctata* (OF Müller, 1774), *O. lactea* (OF Müller,



Figure 2. Maximum Likelihood (RAxML) tree based on concatenated data set of COI, 16S, H3, and 5.8 S rRNA+ITS2. Numbers represent bootstrap support values from the ML analysis.



Figure 3. Bayesian Inference tree based on concatenated data set of COI, 16S, H3, and 5.8 S rRNA+ITS2. Numbers represent Bayesian posterior probabilities.

1774), and *O. xanthodon* (Anton, 1838). The specimen of "*Tingitana minettei decussata*" (nomen nudum) clusters within the *O. xanthodon* clade. The monophyly of *O. lactea* is not statistically supported (bootstrap value of 65). Within *O. xanthodon* there are some nodes with very low support, especially the node which includes "*Tingitana minettei decussata*" (NMBE 549840). *Otala l. murcica* (Rossmässler, 1854) (NMBE-554175 and NMBE-

9

554176 in Figs 2, 3) nests within the *O. lactea* clade. Both, the separate mitochondrial and nuclear tree show the same topology as the concatenated tree. They can be found in the supplementary material (Suppl. materials 1, 2).

The Bayesian Inference analysis of the concatenated data set (Fig. 3) recovered the monophyly of *Alabastrina*. This node is statistically supported (posterior probability of 1). The monophyly of *S. pallaryi* and *Otala* and thus the separation of *S. pallaryi* and *Alabastrina* is fully supported. There is no difference in both types of analyses in the *O. lactea* and the *O. xanthodon* clade. The separate mitochondrial and nuclear trees can be found in the supplementary material (Suppl. materials 3, 4).

Taxonomic accounts

The nomenclature of the parts of the genital organs follows Neubert and Bank (2006) and Neubert (2014). In Table 3, the traits of the genital organs are summarised.

Alabastrina Kobelt, 1904

- 1904 Alabastrina Kobelt, in Rossmässler: Iconographie der Land- & Süsswasser-Mollusken, (2) 11: 33, 132, 194 [type species Helix alabastrites Michaud, 1833 by OD].
- 1904 *Alabastra* Kobelt, in Rossmässler: Iconographie der Land- & Süsswasser-Mollusken, (2) 11: 100.

Currently, this genus is subdivided in six subgenera (Schileyko 2006). This system is more or less completely based on shell characters and only for a few specimens the morphology of the genital organs has been investigated and published. Schileyko (2006: 1794, fig. 2297B, C) shows the genital organs of *Helix hieroglyphicula* Michaud, 1833, which is the type species of *Michaudia* Pallary, 1926 [by original designation]. In his definition of *Alabastrina* sensu lato, he uses the character state "branches of mucus glands before entering common duct form distinct swellings" (Schileyko 2006: 1792). This interesting trait is not seen in any of the *Alabastrina* species investigated by us. Holyoak and Holyoak (2017: 426, Table 1) relegate *Michaudia* into the synonymy of *Otala*, also based on Schileyko's figure arguing with the conformity in the structure of

	A. alabastrites	A. tistutensis	S. pallaryi	O. lactea	O. punctata	O. xanthodon
relative size of the AS	medium	medium	no data	large	large	large
penial flap	yes	yes	no data	no	no	no
relative size of the Fl	short	short	no data	long	medium	long
relationship BC:BCD	1:1	no data	no data	1.5:2	1:1	1.5:2
no. of penial papillae	1	1	no data	2	1	2
penial appendix	yes	yes	no data	no	no	no

Table 3. Traits of genital organs.

the interior of the proximal penis. The assumption by Schileyko (2006) that *Alabastrina* agrees with *Otala* on the presence of two penial papillae is wrong.

Without further comment, Holyoak and Holyoak (2017) consider *Loxana* Pallary, 1899 a separate genus, follow Razkin et al. (2015) in leaving *Atlasica* Pallary, 1917 as a subgenus of *Alabastrina*, and omit *Lechatelieria* Pallary, 1926. Taxon sampling in Razkin et al. (2015) is not sufficient enough to clearly reveal the subgeneric position of *Atlasica*. Based on our anatomical investigation, the genus *Alabastrina* can now be newly characterised using the following traits of the genital organs: Penis with a single penial papilla (PP) with a central pore, distal penis with penial flap (PF), proximal penis with a small penial appendix (PA); epiphallus and flagellum of similar length; mucus glands (MG) multifid, branches very long and slender.

Nomenclatural remark: Kobelt established the names *Alabastra* and *Alabastrina* simultaneously in the register volume of the "Iconographie". In this work, he presented a register on the "System der palaearktischen Binnenconchylien", listing a genus group name together with a single species group name (129 ff.). In the second register (171 ff.), he provided a systematically ordered list with information on all taxa ever published in the "Iconographie", and affiliated these taxa into the new system as outlined before in register 1. Both registers are accompanied by text dealing with zoogeographic considerations and taxonomic remarks.

The name *Alabastra* was used three times exclusively on page 100 (in combination with a species list). The name *Alabastrina* was used on page 33 (zoogeographic context), page 132 (systematic register combined with the species group name *alabastrites*), page 158 (a list of potential members of *Alabastrina* including *alabastrites*), and finally page 194 (amended list of illustrated taxa of *Alabastrina* sensu Kobelt). According to ICZN 24.2.4 we deem Kobelt to act here as First Reviser, because he consequently used the name *Alabastrina* in his registers. We interpret the name *Alabastra* to constitute an erroneous misspelling.

Both genus group names included species lists of differing composition, the name *alabastrites* was always included (loc. cit.). In the first register, the name *Alabastrina* was combined with a single species (p. 132). We consider this act a designation of the type species by the original author (OD); Schileyko's note on the type species selection (2006: 1792) as "monotypy" is erroneous.

Alabastrina alabastrites (Michaud, 1833)

Figs 4–8

- 1833 Helix alabastrites Michaud, Catalogue des testacés vivans envoyés d'Alger par M. Rozet, capitaine au corps royal d'État-Major, au cabinet d'Histoire Naturelle de Strasbourg: 4, figs 6–8 [Oran].
- 1833 Helix soluta Michaud, Catalogue des testacés vivans envoyés d'Alger par M. Rozet, capitaine au corps royal d'État-Major, au cabinet d'Histoire Naturelle de Strasbourg: 3, figs 9, 10 [Oran].



Figure 4. *Alabastrina* type specimens. **A** *Helix soluta*, syntype MHNL 45000679, Oran, Algeria, coll. Michaud, D = 24.15 mm **B** *Helix alabastrites*, syntype MHNL 45000690, Oran, Algeria, coll. Michaud, D = 22.48 mm. All photographs by Kneubühler & Neubert, × 1.5.

Type specimens: *Helix alabastrites*: syntype MHNL 45000690; *Helix soluta*: syntype MHNL 45000679.

Specimens examined: for sequenced specimens, see Table 1.

Description. The range of the shell diameter of the investigated specimens is between 14.93–22.77 mm and shell height is between 10.85–13.45 mm. The shell of this species is pale and often with dark brown stripes. Some individuals do not show any stripes at all (Figs 4B, 6A). There is none to one tooth found in the aperture.

This species has a rather short flagellum which is a bit shorter than the penis. MG are thin and fragile. The epiphallus goes over into the penial lumen without any penial papilla. Parallel but outside of the epiphallus is a penial appendix found. This penial appendix lies next to the epiphallus and is also covered by the penial sheath. It is blind on one side and opens into the penial lumen on the other side (PA in Fig. 5C, D). From there a huge penial papilla (PP) points towards the atrium. The PP is surrounded by massive muscles. In the atrium is a large atrial stimulator found and a smaller is located at the exit of the penis (PF).

Alabastrina tistutensis Galindo, 2018

2018 Alabastrina tistutensis Galindo, Mostra mondiale, Cupra Marittima (2): 22–26.

Type specimen: *Alabastrina tistutensis*: holotype MMM Cupra Marittima (2): 23. Specimens examined: for sequenced specimen, see Table 1.



Figure 5. *Alabastrita alabastrites* (NMBE 549817), Kebdana Mountain, Morocco; **A** shell **B** situs **C** penis **D** penial lumen; D = 21.91 mm, H = 13.36 mm, situs length 27.57 mm (atrium-flagellum). All photographs by Kneubühler, shell \times 1.5.

Description. The shell is pale and characterised by a sharp keel. The aperture is white with a white lip. The mucus glands (MG) are fragile and slender. The flagellum is slightly shorter than the penis. The epiphallus is characterised by longitudinal tissue ridges and goes over into the penial lumen without any penial papilla. Parallel but outside of the epiphallus is a penial appendix found (PA in Fig. 9C). It is together with the epiphal-



Figure 6. *Alabastrita alabastrites* (NMBE 549812), cave Ifri n'Ammar, Morocco; **A** shell **B** situs **C** penis **D** penial lumen; D = 19.72 mm, H = 13.00 mm, situs length 26.27 mm (atrium-BCD). BC lost during dissection. All photographs by Kneubühler, shell × 1.5.

lus covered by the penial sheath. The PA is blind on one side and the other side opens into the penial lumen. This species possesses one penial papilla (PP in Fig. 9C) which is slightly smaller than in *A. alabastrites* but it is clearly visible. A large atrial stimulator is found in the atrium and a smaller stimulator is situated in front of the exit of the penis.



Figure 7. *Alabastrina alabastrites* (NMBE 549813), hills El Batel, Morocco; **A** shell **B** situs **C** penis; D = 17.25 mm, H = 10.85 mm, situs length 13.46 mm (atrium-flagellum). Situs is not complete. All photographs by Kneubühler, shell × 1.5.

Siretia Pallary, 1926

1926 Siretia Pallary, Journal de Conchyliologie, 70: 19.

This genus is characterised by a triangular, toothless aperture, the short upper edge of the shell, its flat form, and by having four dark bands (Pallary 1926). Although *Siretia* has a peculiar shell morphology, Schileyko (2006) considers it as a subgenus of *Alabastrina*. Our phylogenetic analyses reveal it as a separate genus.

Siretia pallaryi (Kobelt, 1909)

Figure 10

- 1909 *Archelix pallaryi* Kobelt, Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft, 41 (3): 134 [Taforalt im Gebiet der Beni Snassen].
- 1914 Archelix pallaryi, Kobelt: in Rossmässler: Iconographie der Europäischen Land- & Süsswasser-Mollusken (2) 20: 21, fig. 2790.



Figure 8. *Alabastrina alabastrites* (NMBE 549816), Etsedda/ Kebdana, Morocco; **A** shell **B** situs **C** penis; D = 22.77 mm, H = 13.45 mm, situs length 36.84 mm (atrium-BCD). BC destroyed. All photographs by Kneubühler, shell \times 1.5.

1926 Siretia pallaryi, Journal de Conchyliologie, 70: 19, figs 5, 6, 8.

Type specimen: Siretia pallaryi: syntype SMF 75926.

Specimens examined: for sequenced specimen, see Table 1.

Description. In Figure 10B, a syntype of *S. pallaryi* from Teforalt (= Taforalt), Morocco (coll. CR Boettger ex Kobelt) is shown. The type specimen is slightly larger than our investigated specimen (Fig. 10A). Both show similar shell morphology and stripe pattern. Unfortunately, our specimen was badly preserved and a juvenile, therefore no proper investigation of the genital organs could be made.

Remarks. Holyoak and Holyoak (2017: 446) attribute this species to A Koch. However, in the description Kobelt explicitly mentions "Koch mss". Therefore, Kobelt is considered the nomenclatural author of this taxon.



Figure 9. *Alabastrina tistutensis* (NMBE 555174), Tiztoutine, Morocco; **A** shell **B** situs **C** penis; D = 19.59 mm, H = 8.74 mm, situs length 13.51 mm (atrium-flagellum). Situs not complete. All photographs by Kneubühler, shell × 1.5.



Figure 10. A *Siretia pallaryi* (NMBE 549815), Kebdana Mountain, Morocco, D = 16.82 mm, H = 8.81 mm; **B** *S. pallaryi* (SMF 75926), Teforalt (= Taforalt), Morocco, coll. CR Boettger, D = 19.38 mm. All photographs by Kneubühler & Neubert, $\times 1.5$.

Otala Schumacher, 1817

- 1817 *Otala* Schumacher, Essai d'un nouveau système des habitations des vers testacés: 58, 191 [type species *Helix lactea* OF Müller, 1774, by subsequent designation Pilsbry, 1895: 323].
- 1904 *Otala (Dupotetia)* Kobelt: in Rossmässler: Iconographie der Europäischen Land- & Süsswasser-Mollusken (2) 11: 158 [type species *Helix dupotetiana* Terver, 1839 by original designation].
- 1918 Alabastrina (Tingitana) Pallary, Bulletin de la Société d' Histoire naturelle de l'Afrique du Nord, 9 (7): 145 [type species Archelix minettei Pallary, 1917 by monotypy].

This genus was recently revised by Holyoak and Holyoak (2017). After examining several hundreds of specimens from Morocco and Algeria, they distinguish five species within the genus *Otala*, i.e., *O. punctata*, *O. lactea*, *O. xanthodon*, *O. tingitana* (Paladilhe, 1875), and *O. hieroglyphicula* (Michaud, 1833). The species formerly attributed to *Tingitana* Pallary, 1918, and *Dupotetia* Kobelt, 1904 (genera which appeared to have species in the area of the Kebdana) are now lumped under *Otala tingitana*. This lumping approach is supported by the molecular study of Helicoidea by Razkin (2015), who revealed that the genus *Tingitana* is nested within *Otala*. In our phylogenetic analysis we included a specimen of the well-known shell form "*Tingitana minettei decussata*", which clustered within the *O. xanthodon* clade thus supporting the results of Razkin (2015) and Holyoak and Holyoak (2017). More taxon sampling is needed to reveal the phylogenetic relationships within *Otala*.

Otala lactea (OF Müller, 1774)

Figs 11–16

Type specimens: Helix lucasii: MNHN IM-2000-31721.

Specimens examined: for sequenced specimens, see Table 1.

Description. The shell of *O. lactea* is characterized by a dark aperture. The shell diameter of the investigated specimens ranges between 27.01–40.81 mm and shell height between 15.77–21.75 mm. This species has a large and thick penial tube. It has two distinct penial papillae with each a large central pore. The distal penial lumen between the large tongue-shaped atrial stimulator and the distal penial papilla (PP2) exhibits longitudinal ridges. The distal penial papilla is located ca. 2 mm distally to the atrium. The penial chamber which is bordered by the two penial papillae ranges between 2–4 mm and is characterised by strong annular tissue folds. There is a short transformation zone between the proximal penial papilla (PP1) and the epiphallus. The epiphallus is characterised by longitudinal tissue ridges. The flagellum is ca. 1.5× the length of the penis. The BCD is ca. double in length as the BC, except for the specimen in Figure 13, where they are approximately the same length. The vagina



Figure 11. *Otala lactea* (NMBE 553246), W Almocageme, Portugal; **A** shell **B** situs **C** penis and atrium; D = 29.82 mm, H = 18.71 mm, situs length 41.34 mm (atrium-BCD). All photographs by Kneubühler, shell × 1.5.

is stout and short. The MG consist of two massive stems which subdivide into ten smaller branches.

Remarks. The analysis includes also specimens of *O. l. murcica* (Fig. 15) from Almería, Spain, which is the type locality. This taxon is characterised by a larger shell and an aperture, which is enlarged and more reflected (Cadevall and Orozco 2016).



Figure 12. *Otala lactea* (NMBE 554174), N Málaga, Spain; **A** shell **B** situs; D = 27.25 mm, H = 18.60 mm, situs length 22.90 mm (atrium-albumin gland); juvenile, BC destroyed. All photographs by Kneubühler, shell \times 1.5.

The morphology of the genital organs shows no difference to the specimens of *O. lactea* investigated from Portugal or Morocco.

In a small area in north-eastern Morocco, another form of *O. lactea* occurs, namely *Helix lucasii* (Fig. 16D). Our investigation of a specimen from this population revealed some differences in the anatomy of the genital organs (Fig. 16C). The penial chamber is much longer than in the other specimens of *O. lactea*. The length of the penial chamber (PP1-PP2) is 4 mm and the length of the distal penial lumen (PP2-AS) is 1.8 mm. The internal structures differ substantially. Here, the inner walls of this tube are filled by numerous fine transverse ridges arranged in a very dense annular pattern. All other specimens seen so far displayed an irregular network of tissue folds in this section of the penis. Additionally the shell is quite large and flat with a comparatively strong basal tooth or strengthened lip.

Otala punctata (OF Müller, 1774)

Figs 17, 18

Specimens examined: for sequenced specimens, see Table 1.

Description. The shell is characterized by a white lip and a basal tooth. This species is characterized by a long and thick penial tube. It has a large penial papilla (PP),



Figure 13. *Otala lactea* (NMBE 555171), Hassi Ouenzga/ Oriental, Morocco; **A** shell **B** situs **C** penis and atrium; D = 22.63 mm, H = 14.85 mm, situs length 34.60 mm (atrium-flagellum). All photographs by Kneubühler, shell × 1.5.

which is located ca. 2 mm distally to the atrium (Figs 17, 18) with a large central pore. The second proximal penial papilla is reduced and inconspicuous. The distal penial lumen between the atrial stimulator and the penial papilla exhibits a few low longitudinal ridges intersected by many small annular folds. The proximal lumen between penial papilla and epiphallus is filled by a network of irregularly shaped folds and small and large ridges. The epiphallus is characterised by longitudinal tissue ridges with a small transformation zone at the proximal end of the penial lumen. The flagellum has approximately the same length as the penis. The vagina is short and stout. The mucus glands (MG) consist of two massive stems which subdivide into 10-12 smaller subsequent branches. The BCD has approximately the same length as the BC. They are ca. $3\times$ the length of the flagellum and the penis. The dominant



Figure 14. *Otala lactea* (NMBE 549951), W Aoulouz, Morocco; **A** shell **B** situs; D = 27.01 mm, H = 15.77 mm, situs length 30.77 mm (atrium-flagellum); juvenile; situs not complete; BC destroyed. All photographs by Kneubühler, shell \times 1.5.

structure in the atrium is a large, folded stimulator, which was also mentioned by De Mattia and Mascia (2011).

Otala xanthodon (Anton, 1838)

Figs 19–23

Specimens examined: for sequenced specimens, see Table 1.

Description. The shell is characterized by a dark aperture with a white and strongly reverted lip. This species possesses one basal tooth. A palatal tooth is found in some specimens. The shell diameters of the investigated specimens range between 21.47–



Figure 15. *Otala lactea* (NMBE 554175), W Almería, Spain; **A** shell **B** situs **C** penis and atrium; D = 31.89 mm, H = 18.23 mm, situs length 57.86 mm (atrium-BCD). All photographs by Kneubühler, shell × 1.5.

27.77 mm and shell height between 13.37–16.04 mm. *Otala xanthodon* has two distinct penial papillae with each a large central pore. The distal penial lumen between the atrial stimulator and the distal penial papilla (PP2) exhibits smooth longitudinal tissue ridges. The penial chamber which is bordered by the two penial papillae is filled by a network of irregularly shaped tissue folds and is ca. 3 mm long. There is a short



Figure 16. *Otala lactea* (NMBE 545594); Etsedda/Kebdana, Morocco; **A** shell **B** situs **C** penis; D = 40.81 mm, H = 21.75 mm, situs length 61.47 mm (atrium-BCD), BC destroyed; **D** *H. lucasii* (syntype MNHN IM-2000-31721), Oran, Algeria, D = 35.4 mm. All photographs by Kneubühler & Neubert, shell original size.

transformation zone between the proximal penial papilla (PP1) and the epiphallus. The epiphallus contains few smooth longitudinal ridges. This species has a large flagellum which is ca. double the length of the penis. The BC is a thin tube and ca. half the length of the BCD. It has two massive mucus glands (MG) which subdivide in four thinner branches of which each again subdivides in two thin branches. The dominant structure in the atrium is a large tongue-shaped stimulator.



Figure 17. *Otala punctata* (NMBE 534228); Makouda, Algeria; **A** shell **B** situs **C** penis; D = 36.02 mm, H = 22.37 mm, situs length 59.77 mm (atrium-BCD). All photographs by Kneubühler, shell original size

"Tingitana minettei decussata"

Figs 24, 25

Specimens examined: *Otala tingitana* (NMBE 510549); for the sequenced specimen of *"Tingitana minettei decussata"* NMBE 549840, see Table 1.

Nomenclatorial note: The name "*decussata* Pallary" is a nomen nudum as already stated by Holyoak and Holyoak (2017: 463). Pallary never made the name available, nor did Llabador (1952). For the latter publication, the provisions of Article 13 ICZN (names published after 1930) rule that every new name must "be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon" or Article 13.1.2. "be accompanied by a bibliographic reference to such a published statement". No such statements are provided by Llabador. This taxon is well known and often treated as a subspecies of *Tingitana minettei* (Pallary, 1917) (see for example Cossignani 2014). The genus *Tingitana* Pallary, 1918 is synonymised with *Otala* by Holyoak and Holyoak (2017).



Figure 18. *Otala punctata* (NMBE 554171); W Málaga, Spain; **A** shell **B** situs **C** penis; D = 30.30 mm, H = 18.05 mm, situs length 70.10 mm (atrium-BC). All photographs by Kneubühler, shell × 1.5.

Description. The shells of "*decussata*" are flat and have a sharply keeled last whorl. The aperture is oval and dark brown inside with a white lip and a strong basal tooth. "*Tingitana minettei decussata*" has a network-like sculpture on its surface (Fig. 25). This is in contrast to *Otala tingitana* with a rather smooth surface and a few weakly developed radial ribs. In this species, the interior of the aperture is brighter and the basal tooth conspicuously smaller. Typically, *O. xanthodon* has a smooth shell with evenly rounded whorls and up to three apertural denticles.

The genital organs of "*decussata*" are characterised by two distinct penial papillae, each with a central pore. The distal penial lumen between the atrial stimulator and the distal penial papilla (PP2) is characterised by a network of irregularly shaped folds with



Figure 19. *Otala xanthodon* (NMBE 549825), Moulouya, Morocco; **A** shell **B** situs **C** atrium and penis; D = 23.13 mm, H = 14.49 mm, situs length 32.68 mm (atrium-BCD). BC destroyed. All photographs by Kneubühler, shell × 1.5.

large and small ridges. The penial chamber exhibits many annular tissue folds and is ca. 3 mm long. Between the proximal penial papilla (PP1) and the epiphallus is a short transformation zone. The epiphallus is characterised by two strong and several smooth longitudinal ridges. The mucus glands consist of two massive stems which subdivide into several thinner branches which again become thinner in the second half. The dominant structure in the atrium is a large tongue-shaped stimulator. There are almost no differences in the inner and outer morphology of the genital organs of "*decussata*" and *O. xanthodon* specimens.



Figure 20. *Otala xanthodon* (NMBE 549826), Moulouya, Morocco; **A** shell **B** situs **C** atrium and PP2 **D** penial chamber; D = 21.47 mm, H = 14.22 mm, situs length 37.23 mm (atrium-BCD). All photographs by Kneubühler, shell × 1.5.

Remarks. According to field observations by R Hutterer, this particular taxon does only occur on top of one mountain in the Kebdana range; comparison with similar specimens illustrated by Cossignani (2014: 109) from Ras el Ma and Tazouta is pending. The distribution area of *O. tingitana/minettei* is far and separated by lowlands, so a position of this taxon as a species in its own right is highly probable. However, as long as topotypic specimens of *O. tingitana* are missing in the genetic analysis, the exact taxonomic position of "*decussata* Pallary" remains unclear. Our results signal a position within or close to *O. xanthodon* rather than to *O. tingitana*.



Figure 21. *Otala xanthodon* (NMBE 549841), Kebdana Mountain, Morocco; **A** shell **B** situs; D = 26.85 mm, H = 15.74 mm, situs length 33.58 mm (atrium-flagellum). Situs not complete. All photographs by Kneubühler, shell × 1.5.



Figure 22. *Otala xanthodon*, Kebdana, Moulouya valley, Morocco; **A** shell from *O. xanthodon* (NMBE 555169), D = 22.33 mm, H = 13.61 mm; **B** shell from *O. xanthodon* (NMBE 555170), D = 23.10 mm, H = 13.37 mm. Kebdana, Djebel Sebaa Reyal/ Rif **C** shell from *O. xanthodon* (NMBE 549843), D = 27.77 mm, H = 16.04 mm. All photographs by Kneubühler, shell × 1.5.



Figure 23. *Otala xanthodon* (NMBE 549820), Guercif, Morocco; **A** shell **B** situs **C** atrium and penis; D = 26.74 mm, H = 15.96 mm, situs length 42.81 mm (atrium-BCD), BC destroyed; **D** *Helix zaffarina* Terver, 1839 (syntype MHNL 45001034), Oran, Algeria, coll. Michaud, D = 29.54 mm. All photographs by Kneubühler & Neubert, shell × 1.5.



Figure 24. *Otala tingitana* (NMBE 510549), Tarzout de Guigou, Morocco, D = 27.42 mm, H = 14.38 mm (specimens from the type locality of *Archelix minettei* Pallary, 1917). All photographs by Kneubühler, shell \times 1.5.



Figure 25. "*Tingitana minettei decussata*" (NMBE 549840), Kebdana, Morocco; **A** shell **B** situs **C** atrium and penis; D = 32.45 mm, H = 16.12 mm, situs length 28.84 mm (atrium-flagellum). Situs not complete. All photographs by Kneubühler, shell × 1.5.

Discussion

The results of our study strongly support the monophyly of the genera *Alabastrina* and *Otala* within the tribe Otalini. *Alabastrina alabastrites* is morphologically as well as genetically clearly separated from the genera *Siretia* and *Otala*. All investigated specimens within *Alabastrina* show the unique trait of the presence of a blind penial appendix. This is an anatomical character, which has never been reported before within the Helicidae. The function of this penial appendix is not known. Schileyko's system which was

based on morphology only, is incorrect as we could demonstrate in our phylogeny that the species *Archelix pallaryi* Kobelt, 1909, which is the type species for the genus *Siretia*, clusters outside the *Alabastrina* clade. We consider this taxon as a separate genus. Anatomical and genetic data for *Helix bailloni* Kobelt, 1888, the type species of *Guilia* Pallary, 1926 also suggest a phylogenetically separate position of this genus (Kneubühler et al. in prep.). The position of *A. tistutensis* within the clade of *A. alabastrites* shows that this extreme local shell form should probably be considered a local subspecies rather than a species in its own rights. Further sampling is necessary to resolve the problem.

The phylogenetic results clearly show that *Siretia* is separated from *Alabastrina*. In the ML analyses *Siretia* forms a lineage separate from *Otala* (Fig. 2; Suppl. materials 1, 2). However, in the Bayesian Inference analyses, *Siretia* clusters within the *Otala* clade (Fig. 3; Suppl. materials 3, 4). Thus, the monophyly of *Otala* is not supported. It cannot be excluded that *Siretia* forms a subgenus or even a synonym of *Otala*. Unfortunately, we cannot present anatomical data for *S. pallaryi* because of the bad preservation of the only specimen we could analyse. More sequence data are necessary to corroborate the monophyly of *Otala* and to resolve the relationships within the *Otala* clade (including *Siretia*). For the time being, *Siretia* is considered here as a separate unit because of the differences in shell shape. Holyoak and Holyoak (2017: 423) regard *Siretia* as a distinct genus within the Otalini.

Otala lactea is characterized by a dark aperture, which clearly differentiates it from O. punctata with a white aperture. We investigated several populations of O. lactea from Morocco, Spain and Portugal and they all cluster together in the phylogenetic analysis. Hesse's (1911) investigations of the outer morphology of the genital organs of Archelix punctata, A. lactea, and A. lucasi showed no difference to our results. In contrast to Holyoak and Holyoak (2017), we could distinguish the species O. lactea and O. punctata without any doubt by their genital anatomy. Otala punctata has one strongly developed penial papilla and a second which is nearly completely reduced, whereas O. lactea has two massive and distinct penial papillae. Unfortunately, Holyoak and Holyoak (2017: 425, Table 1) do not describe the form of the proximal verge (PP1 herein) for each species nor do they provide a drawing. This hampers the interpretation of the data known so far and we agree that more detailed study may be necessary for a reliable comparison of species.

We also investigated specimens of *O. l. murcica* from Almería, Spain; from a genetic point of view there is no difference to the remaining specimens of *O. l. lactea*. The two specimens of *O. l. murcica* included in the analyses from the same population (NMBE-554175 and NMBE-554176 in Figs 2, 3) cluster together with the Portuguese specimen of *O. lactea*, which originates close to the type locality of the neotype of *O. lactea* designated by Holyoak and Holyoak (2017: 446). For this reason we conclude that this subspecies has to be considered a synonym of *O. lactea*.

The specimen from Etsedda, Morocco (NMBE-545594 in Figs 2, 3) clusters as the sister lineage of all investigated *O. lactea* specimens. It shows a slightly different shell morphology and genital anatomy (Fig. 16A, B, C). The shells of this population strongly resemble *Helix lucasii* (syntype shown under Fig. 16D). However, the bootstrap support value for this clade (65) is too low to currently allow the separation as a distinct species or whether it falls within the range of variability of *O. lactea*. More specimens are needed here to corroborate the differences in the anatomical details of the genital organs as well as the separate position on the phylogeny.

"Tingitana minettei decussata" clusters within the specimens of O. xanthodon but with a low support (Figs 2, 3). The genital organs show strong similarities to other O. xanthodon specimens as exemplified by the system of two penial papillae, the short penial chamber, the massive mucus glands, and the large atrial stimulator. However, the shell morphology of this form is clearly different. This could be due to a local adaptation to a rocky habitat since the gastropod shell form is strongly influenced by the substrate the species live on (Goodfriend 1986); specimens with a flat shell can hide more easily in crevices, particularly in limestone. This conflicts with the definition of *Tingitana* by Pallary, who erected this genus for species with a keeled shell. Next to the observation cited above that keeled shells are probably an adaptation to a rocky environment with crevices, juvenile shells of large helicid species often show this phenomenon of a keeled shell (see for example species of *Levantina* Kobelt, 1871, *Codringtonia* Kobelt, 1898, *Isaurica* Kobelt, 1901, etc. (Holyoak and Holyoak 2017)). Consequently, this trait is unsuitable for generic definition; its use even for species delimitation is disputable.

Holyoak and Holyoak (2017) synonymised *H. zaffarina* (a species usually under *Dupotetia*) with *O. xanthodon*. Therefore, we included a specimen that usually would have been identified as *D. zaffarina* in our study (Fig. 23A), and compared the shell with that of the syntype (Fig. 23D). We agree here with the synonymisation of *H. zaffarina* with *O. xanthodon*, because our genetic analyses revealed that this specimen clusters within the specimens of *O. xanthodon*.

Acknowledgements

We are grateful to Estée Bochud (NMBE Switzerland) for support during the anatomical research and technical advice, José Ahuir Galindo (Málaga, Spain) and Adrienne Jochum (NMBE Switzerland) for providing specimens used in this study. RH is grateful to the support of Deutsches Archäologisches Institut (Bonn) and the Institut National des Sciences de l'Archéologie et du Patrimoine (Rabat). We acknowledge the valuable comments of the reviewers B Hausdorf and MT Neiber (both Hamburg) on an earlier draft of this paper.

References

Altekar G, Dwarkadas S, Huelsenbeck JP, Ronquist F (2004) Parallel Metropolis-coupled Markov chain Monte Carlo for Bayesian phylogenetic inference. Bioinformatics 20: 407– 415. https://doi.org/10.1093/bioinformatics/btg427

- Anton HE (1838) Verzeichniss der Conchylien welche sich in der Sammlung von Hermann Eduard Anton befinden. Eduard Anton, Halle, 110 pp. https://doi.org/10.5962/bhl.title.11509
- Bouaziz-Yahiatene H, Pfarrer B, Medjdoub-Bensaad F, Neubert E (2017) Revision of *Massylaea* Möllendorff, 1898 (Stylommatophora, Helicidae). ZooKeys 694: 109–133. https://doi. org/10.3897/zookeys.694.15001
- Cadahia L, Harl J, Duda M, Sattmann H, Kruckenhauser L, Feher Z, Zopp L, Haring E (2014) New data on the phylogeny of *Ariantinae* (Pulmonata, Helicidae) and the systematic position of *Cylindrus obtusus* based on nuclear and mitochondrial DNA marker sequences. Journal of Zoological Systematics and Evolutionary Research 52(2): 163–169. https://doi.org/10.1111/jzs.12044
- Cadevall J, Orozco A (2016) Caracoles y babosas de la península Ibérica y Baleares. Nueva guías de campo. Omega, Barcelona.
- Colgan D, McLauchlan A, Wilson GDF, Livingston SP, Edgecombe GD (1998) Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. Australian Journal of Zoology 46: 419–437. https://doi.org/10.1071/ZO98048
- Cossignani T (2014) African Landshells. L'informatore Piceno, Ancona.
- De Mattia W, Mascia F (2011) *Otala punctata* (O.F. Müller, 1774) (Stylommatophora: Helicidae) in Italy. Iberus 29(1): 39–46.
- Férussac D'Audebard AÉJP, Deshayes GP (1819–1851) Histoire naturelle générale et particulière des mollusques terrestres et fluviatiles, tant des espèces que l'on trouve aujourd'hui vivantes, que des dépouilles fossiles de celles qui n'existent plus; classés d'après les caractères essentiels qui présentent ces animaux et leurs coquilles. J-B Baillière, Paris, 184 pp. [T. 1], 402 pp [T. 2(1)], 1–260, 1–22 [2(2)]. [Atlas 1: 70 pls; Atlas 2: 166 + 5 pls]
- Folmer O, Black M, Hoe W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3(5): 294–299.
- Galindo JA (2018) Three new terrestrial gastropod species and two new subspecies from Morocco. Malacologia, Mostra mondiale, Cupra Marittima 2: 22–26.
- GenBank (2018) National Center for Biotechnology Information, U.S. National Library of Medicine, Rockville Pike. https://www.ncbi.nlm.nih.gov/genbank/ [last accessed 17.12.2018]
- Goodfriend GA (1986) Variation in land-snail shell form and size and its causes: a review. Systematic Zoology 35(2): 204–223. https://doi.org/10.2307/2413431
- Hesse P (1907–1920) Subfamilia Helicinae. In: Iconographie der Land- & Süsswasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten (2) 14 (1/2): 1–64, pl. 361–370 (13 February 1907); (2) 14 (3/4): 65–128, pl. 371–380 (2 September 1907); (2) 14 (5/6): 129–172 + VII pp., pl. 381–390 (12 September 1908); (2) 16 (1/2): 1–42, pl. 421–430 (23 June 1909); (2) 16 (3/4): 43–66, pl. 431–440 (6 June 1910); (2) 16 (5/6): 67–119 + 5 pp., pl. 441–450 (3 August 1911); (2) 23 (1/2): 1–72, pl. 631–640 (October 1915); (2) 23 (3/4): 73–152, pl. 641–650 (11 November 1919); (2) 23 (5/6): 153–262 + 5 pp., pl. 651–660 (24 November 1920). CW Kreidel, Wiesbaden. https://doi.org/10.1016/S0033-3506(09)80188-1
- Holyoak DT, Holyoak GA (2017) A revision of the land-snail genera *Otala* and *Eobania* (Gastropoda, Helicidae) in Morocco and Algeria. Journal of Conchology 42(6): 419–490.

- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17: 754–755. https://doi.org/10.1093/bioinformatics/17.8.754
- Hutterer R, Mikdad A, Ripken TEJ (2011a) Species composition and human exploitation of terrestrial gastropods from Taghit Haddouch, an Early Holocene archaeological site in NE Morocco. Archiv für Molluskenkunde 140: 57–78. https://doi.org/10.1127/arch. moll/1869-0963/140/057-075
- Hutterer R, Eiwanger J, Linstädter J, Mikdad A (2011b) Konsum von Landschnecken im Neolithikum: Neue Daten aus dem östlichen Rif (Marokko). Beiträge zur Paläoanthropologie und Archäozoologie 8: 29–34.
- Hutterer R, Linstädter J, Eiwanger J, Mikdad A (2014) Human manipulation of terrestrial gastropods in Neolithic culture groups of NE Morocco. Quaternary International 320: 83–91. https://doi.org/10.1016/j.quaint.2013.12.006
- Kobelt W (1887–1888). In: Rossmässler EA (Ed.) Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten (2) 3 (1/2): 1–12, pl. 61–70 [15. Apr. 1887]; (2) 3 (3/4): 13–36, pl. 71–80 [6. Oct. 1887]; (2) 3 (5/6): 37–60, pl. 81–90 [10. March 1888]. Kreidel, Wiesbaden.
- Kobelt W (1901–1904) Iconographie der Land- & Süsswasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten von EA Rossmässler (2) 11: 80–264.
- Kobelt W (1909) Diagnose einer neuen Archelix. Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft 41(3): 134–135.
- Kobelt W (1914) Rossmässler's Iconographie der Europäischen Land- & Süsswasser-Mollusken.
 (2) 20, 1–24. [pl. 541–552]
- Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2016) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution. https://doi.org/10.1093/molbev/msw260
- Llabador F (1952) Contribution à l'étude de la faune malacologique terrestre et fluviatile du Rif oriental. Journal de Conchyliologie 92: 93–142. [pl 5]
- Michaud ALG (1833) Catalogue des testacés vivans envoyés d'Alger, par M. Rozet (capitaine au corps royal d'état-major), au cabinet d'histoire naturelle des Strasbourg; notice présentée à la Société d'histoire naturelle de la même ville. Mémoires de la Société d'histoire naturelle de Strasbourg, 1–22.
- Mikdad A, Eiwanger J, Atki H, Ben-Ncer A, Bokbot Y, Hutterer R, Lindstädter J, Moucine T (2000) Recherches préhistoriques et protohistoriques dans le Rif Oriental (Maroc). Beiträge zur Allgemeinen und Vergleichenden Archäologie 20: 109–167.
- Müller OF (1774) Vermium terrestrium et fluviatilium, seu animalium infusoriorum, Helminthicorum et Testaceorum, non marinorum succincta historia. 2. Havinae & Lipsiae, I–XXXVI [= 1–36] + 1–214. https://doi.org/10.5962/bhl.title.46299
- Neiber MT, Hausdorf B (2015) Molecular phylogeny reveals the polyphyly of the snail genus *Cepaea* (Gastropoda: Helicidae). Molecular Phylogenetics and Evolution 93: 143–149. https://doi.org/10.1016/j.ympev.2015.07.022

- Neubert E (2014) Revision of *Helix* (Linnaeus, 1758) in its eastern Mediterranean distribution area, and reassignment of *Helix godetiana* (Kobelt, 1878) to *Maltzanella* (Hesse, 1917) (Gastropoda, Pulmonata, Helicidae). Contribution to Natural History 26: 1–200.
- Neubert E, Bank RA (2006) Notes on the species of *Caucasotachea* C Boettger, 1909 und *Lindholmia* P Hesse, 1919, with annotations to the Helicidae (Gastropoda: Stylommatophora: Helicidae). Archiv für Molluskenkunde 135(1): 101–132. https://doi.org/10.1127/arch. moll/0003-9284/135/101-132
- Neubert E, Korábek O (2015) Comment on Psonis et al. (2015) Evaluation of the taxonomy of *Helix cincta* (Muller, 1774) and *Helix nucula* (Mousson, 1854); insights using mitochondrial DNA sequence data. Journal of Natural History 49: 383–392. https://doi.org/10.10 80/00222933.2015.1021874
- Paladilhe A (1875) Étude sur les coquilles terrestres et fluviatiles rapportées du Maroc par le Dr. Bleicher. Revue et Magasin de Zoologie, pure et appliquée (3^{eme} sér.) 3: 75–101. [pl 9]
- Pallary PM (1899) Deuxième contribution à l'étude de la faune malacologique du Nord-Ouest de l'Afrique. Supplement à "La faune malacologique du Maroc" de A Morelet. Journal de Conchyliologie 46(2) [1898]: 49–170. [pls 5–9; Paris] [9 February].
- Pallary PM (1917) Hélicidées nouvelle du Maroc. Journal de Conchyliologie 63(2): 126-141. [pl 5]
- Pallary PM (1918) Diagnoses d'une cinquantaine de mollusques terrestres nouveaux du Nord de l'Afrique. Bulletin de la Société d'Histoire naturelle de l'Afrique du Nord 9(7): 137–152.
- Pallary PM (1926) Compléments à la faune malacologique de la Berbérie. Journal de Conchyliologie 70(1): 1–50. [pls 1–8]
- Pallary PM (1936) Deuxième complément a la faune malacologique de la Berbérie. Journal de Conchyliologie, 1^{er} Trimestre, 32–39.
- Pilsbry HA (1895) Manual of Conchology, structural and systematic, with illustrations of the species. By George W Tryon, Jr. Second series: Pulmonata, vol 9. (Helicidæ, vol. 7), part 36, frontispiece. Guide to the study of Helices. Conchological Section, Academy of Natural Sciences of Philadelphia, Philadelphia, 161–366. [pls 41–71]
- Pfeffer G (1930) Zur Kenntnis tertiärer Landschnecken. Geologische und Paläontologische Abhandlungen, Jena (NF) 17(3): 3–230 (153–380).
- Psonis N, Vardinoyannis K, Mylonas M, Poulakakis N (2013) Evaluation of the taxonomy of *Helix cincta* (Muller, 1774) and *Helix nucula* (Mousson, 1854); insights using mitochondrial DNA sequence data. Journal of Natural History 49: 383–392. https://doi.org/10.10 80/00222933.2013.825023
- Razkin O, Gómez-Moliner BJ, Prieto CE, Martínez-Ortí A, Arrébola R, Muñoz B, Chueca LJ, Madeira MJ (2015) Molecular phylogeny of the western Palaearctic Helicoidea (Gastropoda, Stylommatophora). Molecular Phylogenetics and Evolution 83: 99–117. https:// doi.org/10.1016/j.ympev.2014.11.014
- Ronquist F, Huelsenbeck JP (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574. https://doi.org/10.1093/bioinformatics/btg180
- Rossmässler EA (1854) Iconographie der Land-und Süsswasser-Mollusken Europa's, mit vorzüglicher Berücksichtigung kritischer und noch nicht abgebildeten Arten. Hermann Costenoble, Leipzig. Band 3, Heft 1–2, 139 pp. [pl 61–88]

- Rour E, Chahlaoui A, van Goethem JL (2002) Etat actuel des connaissances de la malacofaune terrestre du Maroc. Bulletin de l'Institut Royal des Science Naturelle de Belgique, Biologie, 72: 189–199.
- Schileyko AA (2006) Treatise on recent terrestrial pulmonate molluscs. Part 13. Helicidae, Pleurodontidae, Polygyridae, Ammonitellidae, Oreohelicidae, Thysanophoridae. Ruthenica, Supplement 2, Moscow, 1765–1906.
- Schumacher CF (1817) Essai d'un nouveau système des habitations des vers testacés. Schultz, Copenhagen, [1–3], 1–287. [pls 1–22]
- Simon C, Frati F, Beckenbach A, Crespi B, Liu H, Flook P (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Annals of the entomological Society of America 87(6): 651–701. https://doi.org/10.1093/aesa/87.6.651
- Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22(21): 2688–2690. https://doi.org/10.1093/bioinformatics/btl446
- Terver AP (1839) Catalogue des mollusques terrestres et fluviatiles, observés dans les possessions françaises au nord de l'Afrique, publié par M Terver. J-B Baillière, Paris & Savy, Lyon, 1–40. [pls 1–4]
- Walther F, Neiber MT, Hausdorf B (2016) Species complex or complex species? Integrative taxonomy of the land snail genus *Rossmaessleria* (Gastropoda, Helicidae) from Morocco and Gibraltar. Systematics and Biodiversity 14: 394–416. https://doi.org/10.1080/147 72000.2016.1150905

Supplementary material I

Maximum Likelihood (RAxML) tree based on mitochondrial data set of COI and 16S

Authors: Jeannette Kneubühler, Rainer Hutterer, Beat Pfarrer, Eike Neubert Data type: PDF file

Explanation note: Numbers represent bootstrap support values from the ML analysis. Copyright notice: This dataset is made available under the Open Database License

(http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zookeys.843.32867.suppl1
Supplementary material 2

Maximum Likelihood (RAxML) tree based on nuclear data set of H3 and 5.8 S rRNA+ITS2

Authors: Jeannette Kneubühler, Rainer Hutterer, Beat Pfarrer, Eike Neubert Data type: PDF file

Explanation note: Numbers represent bootstrap support values from the ML analysis. Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zookeys.843.32867.suppl2

Supplementary material 3

Bayesian Inference tree based on mitochondrial data set of COI and 16S

Authors: Jeannette Kneubühler, Rainer Hutterer, Beat Pfarrer, Eike Neubert Data type: PDF file

Explanation note: Numbers represent Bayesian posterior probabilities.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zookeys.843.32867.suppl3

Supplementary material 4

Bayesian Inference tree based on nuclear data set of H3 and 5.8 S rRNA+ITS2

Authors: Jeannette Kneubühler, Rainer Hutterer, Beat Pfarrer, Eike Neubert Data type: PDF file

Explanation note: Numbers represent Bayesian posterior probabilities.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zookeys.843.32867.suppl4

RESEARCH ARTICLE



New genera, a new species, and a key to the genera of Ashieldophyinae (Acari, Eriophyoidea) from India

Samiran Chakrabarti¹, Ramkrishna Pandit², Surajit Sur¹

Post-Graduate Department of Zoology, Vidyasagar College, 39 Sankar Ghosh Lane, Kolkata 700006, India
Department of Zoology, Mahadevananda Mahavidyalaya, Barrackpore, Kolkata 700120, India

Corresponding author: Samiran Chakrabarti (chakrabarti32b@gmail.com)

Academic editor: Enrico de Lillo Received 14 August 2018 Accepted 17 February 2019 Published 9 I	May 2019
http://zoobank.org/41942C01-F21A-4B77-B36F-2CCCF1308F87	

Citation: Chakrabarti S, Pandit R, Sur S (2019) New genera, a new species, and a key to the genera of Ashieldophyinae (Acari, Eriophyoidea) from India ZooKeys 843: 39–49. https://doi.org/10.3897/zookeys.843.29078

Abstract

Two new genera, *Brevishieldophyes* Chakrabarti & Pandit, **gen**. **n**. and *Mesoshieldophyes* Chakrabarti & Pandit, **gen**. **n**., and a new species *Mesoshieldophyes varecae* Chakrabarti & Pandit, **sp**. **n**. are described. These mites are leaf vagrants. The morphological characters of the afore-mentioned genera and those of *Ashieldophyes* Mohanasundaram are compared. A key for separating the genera within the subfamily Ashieldophyinae is provided. The diagnostic characters of the subfamily Ashieldophyinae are also revised.

Keywords

Ashieldophyes, Brevishieldophyes gen. n., comparison, descriptions, Mesoshieldophyes gen. n., Mesoshieldophyes varecae sp. n., Brevishieldophyes glochidionae comb. n.

Introduction

Ashieldophyes pennadamensis Mohanasundaram, 1984, infesting Casearia tomentosa Roxb. (Salicaceae) from near the Pennadam Sugar Factory, Arcot district, Tamil Nadu, south India, was the type species for the genus Ashieldophyes Mohanasundaram within the new family Ashieldophyidae Mohanasundaram. Later, the family Ashieldophyidae was made one of the subfamilies (Ashieldophyinae) of the Eriophyidae Nalepa (1898) because a small prodorsal shield was actually observed on the propodosoma of the mite (Amrine and Stasny 1994; Amrine 1996; Amrine et al. 2003). A second species, *Ashieldophyes glochidionae* Chakrabarti & Pandit, 2009, infesting *Glochidion multiloculare* (Rottler ex Willd.) Voigt (Phyllanthaceae) from Lataguri Forest, Jalpaiguri, West Bengal, was described in this taxon.

During periodical samplings for exploration of eriophyoid mite diversity in West Bengal & Assam, further samples of eriophyoids infesting *Casearia vareca* Roxb. and *C. glomerata* Roxb. were collected. Examination of those specimens allowed establishing two new genera, *Mesoshieldophyes* Chakrabarti & Pandit, gen. n. for accommodating *Mesoshieldophyes varecae* Chakrabarti & Pandit, sp. n. and *Brevishieldophyes* Chakrabarti & Pandit, gen. n. for reassigning *A. glochidionae* in the Ashieldophyinae.

Materials and methods

Eriophyoid mites were collected and studied as described by Chakrabarti et al. (2017). The terminology and classification given by Lindquist (1996) and Amrine et al. (2003), respectively are followed here. The specimens were examined with a phase contrast Leica DM3000 microscope and photographs were taken with Leica DFC295 camera. All measurements were made following Amrine and Manson (1996) and de Lillo et al. (2010), and are given in micrometres (µm). Measurements and means are rounded off to the nearest integer and refer to the length of the morphological characters unless specified otherwise. Drawings were made following de Lillo et al. (2010) and Amrine et al. (2003). In the text, measurements of the holotype are followed by the range of measurements of the paratypes plus holotype given in parentheses. All type specimens are now deposited in the collection of the Post-Graduate Department of Zoology, Vidyasagar College, Kolkata 700006, India. After publication, holotypes and paratypes will be deposited in public institutions: one slide with paratypes of each species will be deposited to the National Pusa Collection, Indian Agricultural Research Institute, New Delhi; the holotype and the remaining paratypes will be deposited in the National Zoological Collection, Zoological Survey of India, Kolkata.

Taxonomy

Ashieldophyes Mohanasundaram, 1984 http://zoobank.org/9A73DBEB-3C29-44D3-89DF-B349D0C8F895

Diagnosis. Prodorsal shield small and oval shaped; scapular tubercles absent but with very short scapular setae *sc*, placed on lateral margins, directed laterally; pedipalp genual setae *d* present and simple; femoral setae *bv* of leg I present; genual setae *l*" of leg II present; coxae with setae *1b*; female genitalia located between coxae II; genital cover flap lacks ridges.

Characters	Ashieldophyes	Brevishieldophyes	Mesoshieldophyes
Body	Vermiform	Fusiform	Fusiform
Pedipalp genual setae d	Present	Present	Absent
Prodorsal shield	Small, oval shaped	Small, sickle shaped	Semi-circular, comparatively larger.
Scapular tubercles	Absent	Absent	Absent
Scapular setae <i>sc</i>	Present (very short)	Absent	Absent
Femoral setae <i>bv</i> on leg I	Present	Present	Absent
Solenidion ω	Blunt	Knobbed	knobbed
genual seta <i>l''</i> on Leg II	Present	Present	Absent
Dorsal and ventral semiannuli	Equal number, smooth	Equal number, smooth	Equal number, granular
Seta 1b	Present	Absent	Present

Table 1. Data set for some morphological characters of *Ashieldophyes*, *Brevishieldophyes*, and *Mesoshiel-dophyes*.

Type species. Ashieldophyes pennadamensis Mohanasundaram, 1984.

Remarks. Ashieldophyes Mohanasundaram, 1984, Brevishieldophyes Chakrabarti & Pandit, gen. n., and Mesoshieldophyes Chakrabarti & Pandit, gen. n. belong to the subfamily Ashieldophyinae of family Eriophyidae in having small or moderately developed shield, lacking opisthosomal setae d and e, coxae widely separated anteriorly, female genitalia appressed to the coxae and with a triangular cover flap. These three genera can easily be separated by the characters given in Table 1 and in the key provided below. The genus is monotypic.

Ashieldophyes pennadamensis Mohanasundaram, 1984

http://zoobank.org/D84AC07F-CD6A-42E1-9E42-EA6782545674 Fig. 1 AD1, CG1

Ashieldophyes pennadamensis Mohanasundaram, 1984, Oriental Insects, 18: 251–252.

Diagnosis. Body vermiform; pedipalp genual seta *d* present; prodorsal shield small and oval; scapular tubercles absent but with very short setae *sc*; legs with all usual setae; solenidion ω blunt; opisthosoma with equal number of smooth dorsal and ventral semiannuli; setae *1b* present.

Description. Female (n = 20). Body vermiform, brown colour in life, dorso-ventrally flattened; 250 (175–250) and 40 (39–46) wide. **Gnathosoma** 15 (14–15) projecting obliquely down-curved, dorsal pedipalp genual setae d 1 (1–2); chelicerae 13 (13–15). **Prodorsal shield** small, oval-shaped, without lobe, 9 (9–10) and 23 (22–23) wide, lacking scapular tubercles but with very short scapular setae *sc*, placed on lateral margin and directed laterally. **Leg I** from base of trochanter 20 (20–21), femur 7 (7–8), femoral setae *bv* 7 (7–8), genu 3 (2–3), genual setae *l''* 20 (21–23), tibia 5 (3–5), tibial setae *l'* 15 (12–15), tarsus 5 (3–5), tarsal setae *ft'* and *ft''* both 12 (10–12), solenidion ω 4 (3–4), straight and blunt; empodium *em* simple, 4-rayed; setae *u'* 2 (2–3). **Leg II**



Figure 1. Female: Antero-dorsal region AD and coxigenital region CG ADI and CGI of *Ashieldophyes pennadamensis* AD2 and CG2 of *Brevishieldophyes glochidionae* AD3 and CG3 of *Mesoshieldophyes varecae*.

from base of trochanter 18 (18–20); femur 6 (5–6), femoral setae *bv* 5 (5–6), genu 2 (2–3), genual setae l'' 23 (20–23), tibia 3 (3–4), tibial setae l' absent, tarsus 4 (3–4), solenidion ω 8 (7–8), straight and blunt; empodium *em* simple, 4-rayed; tarsal setae *ft'* 8 (8–10) and *ft''* 12 (10–12), setae *u'* 2 (2–3). **Coxigenital area** smooth; broadly joined, sternal line absent, coxa I widely separate, setae *1b* 2 (2–3) and 5 (5–6) apart, setae *1a* 8 (8–9) and 7 (7–8) apart, setae *2a* 13 (13–15) and 18 (18–20) apart. **Opisthosoma** dorsally flat, smooth, with equal number of dorsal and ventral semiannuli, 21 (20–21); setae *c2* 10 (7–11) on ventral semiannulus 2 (2–3), setae *d* and *e* absent, setae *f* 14 (12–15) on ventral semiannulus 7 (6–7) from rear margin; setae *h1* absent, setae *h2* 12 (12–14). **Genital cover flap** 10 (9–11) and 16 (17–18) wide, triangular and smooth; setae *3a* 8 (6–8). **Internal genitalia** apodeme short, spermathecae rounded with short funnel-like spermathecal tubes.

Specimens examined. India: Tamil Nadu: South Arcot District, near Pennadam Sugar Factory, 16.VIII.1981, 2 females from *C. tomentosa*, coll. M. Mohanasundaram, coll. no. 427 (TNAU); West Bengal: North 24-Parganas, Madral, 12.VIII.2005, many females and nymphs from *C. tomentosa*, coll. R Pandit, coll. nos. 1182–1184/19/2005.

Distribution. India: Tamil Nadu & West Bengal.

Relation to the host plant. The mites inhabit the under surface of leaves as vagrants without showing symptoms of damage to the host plant. **Remarks.** This species is so far known only from its type locality and here reported for the first time from West Bengal.

Brevishieldophyes Chakrabarti & Pandit, gen. n. http://zoobank.org/16667767-867C-4329-A2F9-CF791F511F0B

Diagnosis. Body fusiform, dorso-ventrally flattened. Gnathosoma short, downwardly curved, cheliceral stylet short; prodorsal shield small and sickle-shaped; scapular tubercles and scapular setae sc lacking; pedipalp genual setae d present and simple; coxae without setae 1b; femoral setae bv of leg I present; genual setae l'' of leg II present; empodium simple; female genitalia appressed to the coxae, genital cover flap smooth, triangular, located between coxae II; apodeme normal in length.

Type species. *Ashieldophyes glochidionae* Chakrabarti & Pandit, 2009. The genus is monotypic.

Etymology. *Brevi* derived from the adjective Latin word *brevis* meaning short (in relation to prodorsal shield) and *ophyes* derived from *eriophyes* meaning *erion* = wool + phyes = a grower/maker.

Gender. Masculine.

Brevishieldophyes glochidionae (Chakrabarti & Pandit, 2009), comb. n. http://zoobank.org/33D1FFB7-997E-495E-AD21-EF1EDB27CB2B Fig. 1AD2, CG2

Ashieldophyes glochidionae Chakrabarti & Pandit, 2009, International Journal of Acarology, 15:163–164.

Diagnosis. Body fusiform; pedipalp genual seta d present; prodorsal shield small and sickle shaped; scapular setae *sc* absent; legs with all usual setae; solenidion ω knobbed; opisthosoma with equal number of smooth dorsal and ventral semiannuli; setae *1b* absent.

Specimens examined. India: West Bengal: Jalpaiguri, Lataguri forest, 15.X.2004, many females and nymphs from *G. multiloculare*, coll. R Pandit. coll. nos. 1275–1279/45/2004. Type material of *A. glochidionae* Meghalaya: Burnihat, 18.X.1985, many females and nymphs, from *C. glomerata*, coll. B Das, coll. nos. 967–971/61/1985.

Distribution. India: West Bengal & Meghalaya.

Relation to the host plant. The mites inhabit the under surface of leaves as vagrants without showing symptoms of damage to the host plant.

Remarks. The original report of *B. glochidionae* from *G. multiloculare* needs further confirmation because this mite species and other two Ashieldophyinae have been collected subsequently from plants of the genus *Casearia* (Salicaceae).

Mesoshieldophyes Chakrabarti & Pandit, gen. n.

http://zoobank.org/7227C05D-E910-44EE-AC65-49CACF572032

Diagnosis. Body fusiform, dorso-ventrally flattened. Gnathosoma short, obliquely down-curved, cheliceral stylet short; pedipalp genual setae d absent; prodorsal shield semi-circular without any lobe, lacking scapular tubercles and scapular setae sc; femoral setae bv of leg I and genual setae l'' of leg II absent; coxae with setae 1b; dorsal and ventral semiannuli with granules; female genitalia appressed to the coxae; genital cover flap triangular and smooth; empodium simple; apodeme short in length.

Type species. Mesoshieldophyes varecae Chakrabarti & Pandit, sp. n.

This genus is monotypic.

Etymology. The genus name *Mesoshieldophyes* is derived from *meso* = middle, referring to the medium size of prodorsal shield and *phyes* derived from *eriophyes* meaning *erion* = wool + *phyes*, a grower/maker.

Gender. Masculine.

Remarks. The size of the prodorsal shield in this genus is larger than that in the other two genera of this subfamily.

Mesoshieldophyes varecae Chakrabarti & Pandit, sp. n.

http://zoobank.org/E19A73E2-8A4C-4ABD-8C2F-4FC2DDFBC135 Figs 1AD3, CG3, 2, 3

Diagnosis. Body fusiform; pedipalp genual seta *d* absent; prodorsal shield semi-circular; scapular setae *sc* absent; femoral setae *bv* on leg I absent; genual setae *l*" on leg II absent; solenidion ω knobbed; opisthosoma with equal number of granulated dorsal and ventral semiannuli; setae *1b* present.

Description. Female (n=12). Body fusiform, yellow colour in life, dorso-ventrally flattened; 140 (120-145) and 50 (45-50) wide. Gnathosoma 15 (14-15) projecting obliquely down-wards, dorsal pedipalp genual setae d absent, setae $ep \ 1 \ (1-2)$; chelicerae 13 (13-15). Prodorsal shield semicircular, without lobe, 14 (18-20) and 43 (40–43) wide with granules, lacking scapular tubercles and setae sc. Leg I from base of trochanter 20 (20-21), femur 7 (7-8), femoral setae bv absent, genu 3 (2-3), genual setae l" 20 (21–23), tibia 4 (3–4), tibial setae l' 10 (10–12), tarsus 5 (3–5), tarsal setae ft' and ft" both 12 (10–12), solenidion ω 4 (3–4), straight and knobbed; empodium em 4 (4–5), simple, 4-rayed; setae u' 2 (2–3). Leg II from base of trochanter 18 (18–20); femur 6 (5–6), femoral setae bv 5 (5–6), genu 2 (2–3), genual setae l" absent, tibia 3 (3-4), tibial setae l' absent, tarsus 4 (3-4), tarsal setae ft' 8 (8-10), ft" 12 (10-12); solenidion ω 8 (7–8), straight and knobbed; empodium *em* 4 (4–5), simple, 4-rayed; setae u' 2 (2–3). **Coxigenital area** smooth; sternal line absent, coxae widely separated, setae 1b 2 (2-3) and 5 (5-6) apart, setae 1a 8 (8-9) and 7 (7-8) apart, setae 2a 13 (13-15) and 18 (18-20) apart. Opisthosoma dorsally flat, with equal number of dorsal and ventral semiannuli, 21 (20-21), both dorsal and ventral semiannuli ornamented with fine granules; setae c2 10 (7–11) on ventral semiannulus 2 (2–3), setae d and e absent,



Figure 2. *Mesoshieldophyes varecae*, Female. Abbreviations **CG** coxigenital region **D** dorsal view of body; **em** empodium **IG** Internal genitalia **LO** Dorsal and ventral annuli.

setae f 14 (12–15) on ventral semiannulus 7 (6–7) from rear margin; setae h1 absent, setae h2 12 (12–14). **Genital cover flap** 6 (5–6) and 16 (17–18) wide, triangular and smooth; setae 3a 7 (6–7). **Internal genitalia** apodeme short, spermathecae globose with short, funnel-like spermathecal tubes.

Male. Not observed.

Type host plant. Casearia vareca Roxb. (Salicaceae).

Relation to the host plant. The mites inhabit the under surface of leaves as vagrants without showing symptoms of damage to the host plant.

Type locality. India: West Bengal: Darjeeling, Bengdubi Forest (26°42'30.1"N, 88°25'36.7"E), 163 m above sea level, 03.II.2015, coll. S Chakrabarti, R Pandit, S Sarkar.



Figure 3. *Mesoshieldophyes varecae*, Female **A** prodorsal shield with dorsal annuli **B** genital cover flap **C** entire dorsal body **D** posterior part of opisthosoma with setae *f* and *h2*.

Type material. Holotype: female marked on slide (no. 1294/N11/2015); paratypes: 2 females on slide bearing holotype and 36 females, larvae and nymphs on 10 slides (nos. 1295–1304/N11/2015).

Etymology. The species name *varecae* is from the specific designation of the host plant in the genitive case.

Key to the genera of subfamily Ashieldophyinae

1	Body vermiform, scapular setae sc present; femoral setae bv on leg I and gen-
	ual setae <i>l</i> " on leg II present, on Salicaceae
_	Body fusiform, scapular setae <i>sc</i> lacking 2
2	Prodorsal shield small, sickle shaped; coxal setae 1b lacking; femoral
	setae bv on leg I and genual setae l'' on leg II present, on Salicaceae &
	Phyllanthaceae Brevishieldophyes Chakrabarti & Pandit, gen. n.
_	Prodorsal shield moderate, semicircular; coxal setae 1b present; femoral setae
	<i>bv</i> of leg I and genual setae <i>l</i> " of leg II lacking, on Salicaceae

Subfamily Ashieldophyinae Mohanasundaram (1984)

Diagnosis. Prodorsal shield poorly developed to moderately developed, lacking scapular tubercles, scapular setae *sc* absent but if present very short; sternal line absent; coxae widely separated anteriorly; legs with all segments, setae *bv* on leg I and genual setae l'' on leg II may or may not be present; opisthosoma lacking setae *d* and *e* but *c2* and *f* present; genitalia appressed to the coxae, genital cover flap triangular; genital apodeme curved and abbreviated and spermathecae globose with short spermathecal tubes.

Acknowledgements

Authors extend their thanks to Prof AP Das, Department of Botany, University of North Bengal for identification of the host plant, *Casearia vareca*. Thanks to the Ministry of Environment, Forest & Climate Change, Government of India, New Delhi [Grant no. 22018/05/2010-CS (Tax)] and to the University Grants Commission, New Delhi (Grant no. PSW-111/12-13 ERO) for partially financing the work. Authors (SC and SS) gives thanks to the Principal, Vidyasagar College, Kolkata and RP to the Principal, Mahadevananda Mahavidyalaya, Barrackpore for logistical support. The authors gratefully acknowledge the suggestions made by the reviewers, particularly Prof JW Amrine Jr for improving the earlier versions of this manuscript.

References

- Amrine Jr JW (1996) Key to the World Genera of the Eriophyoidea (Acari: Prostigmata). Indira Publishing House, West Bloomfield, 186 pp.
- Amrine Jr JW, Manson DCM (1996) Preparation, mounting and descriptive study of Eriophyoid mites. In: Lindquist EE, Sabelis MW, Bruin J (Eds) Eriophyoid mites. Their Biology, Natural Enemies and Control. World Crop Pests, 6, Elsevier Science Publishers, Amsterdam, The Netherlands, 383–396. https://doi.org/10.1016/S1572-4379(96)80023-6
- Amrine Jr JW, Stasny TA (1994) Catalog of Eriophyoidea (Acarina: Prostigmata) of the world. Indira Publishing House, West Bloomfield, 798 pp.
- Amrine Jr JW, Stasny TA, Flechtmann CHW (2003) Revised key to the world genera of the Eriophyoidea (Acari: Prostigmata). Indira Publishing House, West Bloomfield, 244 pp.
- Chakrabarti S, Pandit RK (2009) Two new genera and four new species of eriophyoid mites (Acari: Eriophyoidea) from sub-Himalayan West Bengal, India. International Journal of Acarology 35(2): 161–168. https://doi.org/10.1080/01647950902984544
- Chakrabarti S, Sur S, Roy S, Sarkar S (2017) Two new genera and two new species of eriophyoid mites (Acari: Eriophyoidea) from North Bengal, India. Zootaxa 4236(1): 172–182. https://doi.org/10.11646/zootaxa.4236.1.10
- de Lillo E, Craemer C, Amrine Jr JW, Nuzzaci G (2010) Recommended procedures and techniques for morphological studies of Eriophyoidea (Acari: Prostigmata). Experimental and Applied Acarology 51(1–3): 283–307. https://doi.org/10.1007/s10493-009-9311-x

- Lindquist EE (1996) External anatomy and notation of structures. In: Lindquist EE, Sabelis MW, Bruin J (Eds) Eriophyoid Mites – Their Biology, Natural Enemies and Control. World Crop Pests, 6. Elsevier Science Publishers, Amsterdam, 3–31. https://doi.org/10.1016/ S1572-4379(96)80023-6
- Mohanasundaram M (1984) New eriophyid mites from India (Acarina: Eriophyoidea). Oriental Insects 18(1): 251–283. https://doi.org/10.1080/00305316.1984.10432206
- Nalepa A (1898) Zur Kenntniss der Gattung *Trimerus* Nal. Zoologische Jahrbuecher 11(5): 405–411. [pl. 24]

Supplementary material I

COL

Authors: Samiran Chakrabarti, Ramkrishna Pandit, Surajit Sur

Data type: image

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zookeys.843.29078.suppl1

Supplementary material 2

Morphological images 1

Authors: Samiran Chakrabarti, Ramkrishna Pandit, Surajit Sur

Data type: image

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zookeys.843.29078.suppl2

Supplementary material 3

Morphological images 2

Authors: Samiran Chakrabarti, Ramkrishna Pandit, Surajit Sur

Data type: image

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zookeys.843.29078.suppl3

RESEARCH ARTICLE



Review of the genus Stigmus Panzer (Hymenoptera, Crabronidae) in China, with description of five new species from the Oriental and Palearctic Regions

Nawaz Haider Bashir¹, Qiang Li¹, Li Ma¹

I Department of Entomology, College of Plant Protection, Yunnan Agricultural University, Kunming, Yunnan, 650201, China

Corresponding author: Qiang Li (liqiangkm@126.com); Li Ma (maliwasps@aliyun.com)

Academic editor: Michael Ohl	Received 24 November 2018 Accepted 1 April 2019 Published 9 May 2015			
http://zoobank.org/7779AA40-DECB-4732-B27A-61C9AD9695C5				

Citation: Bashir NH, Li Q, Ma L (2019) Review of the genus *Stigmus* Panzer (Hymenoptera, Crabronidae) in China, with description of five new species from the Oriental and Palearctic Regions. ZooKeys 843: 51–69. https://doi. org/10.3897/zooKeys.843.31885

Abstract

Five new species of the genus *Stigmus*: *S. capoblongus* Bashir & Ma, **sp. n.**, *S. denticorneus* Bashir & Ma, **sp. n.**, *S. fronticoncavus* Bashir & Ma, **sp. n.**, *S. interruptus* Bashir & Ma, **sp. n.** and *S. lobomelanicus* Bashir & Ma, **sp. n.** are described and illustrated from China. Also, a key to the species of *Stigmus* Panzer occurring in China is provided.

Keywords

Hymenoptera, new species, Pemphredoninae, Stigmus

Introduction

The genus *Stigmus* Panzer was erected by Panzer (1804) on the basis of type species *Stigmus pendulus* Panzer. At present 25 species and 4 subspecies are described worldwide, of which the highest number of species is known from the Nearctic Region (10 species and 2 subspecies), followed by the Palearctic Region (7 species); 4 species and 2 subspecies were found in the Oriental Region (of which 3 species and 2 subspecies were in China), 2 species in Neotropical Region, 1 species in the Palearctic and Oriental Regions, and 1 species in the Nearctic and Neotropical Regions (Morawitz 1864; Tsuneki 1954, 1977; Kolesnikov 1977; Allen 1987; Budrys 1987, 1995; Uffen 1997, 1998; Jones 2001; Pulawski 2018). Recently, *Stigmus eurasiaticus* was well described by Mokrousov from Russia (Mokrousov 2017).

The diagnostic characteristics that differentiate *Stigmus* from other genera in Pemphredonini are the presence of occipital carina; mandibles in the male bidentate, in the female uni-, bi-, or usually tridentate; vertex micropore field (opaque area) present; labrum subtriangular, pentagonal or trapeziform; face with a shallow scapal basin; interantennal tubercle absent; clypeus of male with silvery dense setae; eyes broadly separated, pitted grooves along orbits narrow or absent; head moderately developed behind eyes; pronotum with a transverse carina; notauli indicated or developed; omaulus well developed (only in *S. solskyi* A. Morawitz is it invisible against the background of a wrinkled mesopleuron sculpture); no definitive episternal sulcus; stigma large, two submarginal cells; hindwing media diverging before or beyond cu-a, hindwing median cell normal size; petiole at least twice its diameter; and female pygidial plate present (Valkeila 1956; Krombein 1973; Bohart and Menke 1976; Finnamore 1995).

In the present study, five new species of genus *Stigmus* Panzer are described and illustrated. A key to the species of the genus *Stigmus* reported from China is also provided.

Materials and methods

The specimens examined in this study belong to the following institutions: Insect Collections of China Agricultural University, Beijing, P. R. China (CAU); Insect Collections of Yunnan Agricultural University, Kunming, Yunnan, P. R. China (YNAU); and Parasitic Hymenoptera Collection of Zhejiang University, Hangzhou, Zhejiang Province, P. R. China (ZJU).

The specimens were observed and illustrated with the help of an Olympus stereomicroscope (SZ Series, Japan) with an ocular micrometer. For the terminology we mainly followed Bohart and Menke (1976). The abbreviations in the text are as follows: BL, body length; HLD, head length in dorsal view (the distance from frons to occipital margin in the middle); HLF, head length in frontal view (the distance from vertex to clypeal margin in the middle); HW, head width (dorsal view, maximum); EW, eye width (lateral view, maximum); EWd, eye width (frontal view, maximum); TW, gena width (lateral view, maximum); EL, eye length (lateral view, maximum); POD, postocellar distance (distance between inner margins of hind ocelli); OOD, ocellocular distance (distance between outer margin of hind ocellus and nearest inner orbit); OCD, ocello-occipital distance (distance between posterior margin of hind ocellus and occipital margin, dorsal view); PW, petiole width (dorsal view, in the middle); PL, petiole length (lateral view); WTI, maximum width of metasomal tergum I (dorsal view); LTI, maximum length of metasomal tergum I (dorsal view).

Key to the species of Stigmus Panzer from China

PR and OR represent Palearctic and Oriental Regions, respectively.

Females (unknown for *S. capoblongus* sp. n)

1	Clypeus deeply impressed, not produced (OR) S. fronticoncavus sp. n.
_	Clypeus flat or slightly convex, slightly or strongly produced2
2	Scrobal suture inconspicuous, lacking or just a single weak carina (PR)
_	Scrobal suture narrow or broad, slenderly or distinctly crenate (OR)
3	Ventral surface of petiole shiny, without carina S. kansitakuanus Tsuneki
_	Ventral surface of petiole with a few strong longitudinal carinae medially and
	posteriorly
4	Ventral gena with large dense punctures mixed with several irregular rugae later-
	ally; lateral surface of petiole with several irregular rugae and two strong lateral
	carinae medially and posteriorly
_	Ventral gena shiny, smooth; lateral surface of petiole with a few strong longitudi-
	nal carinae medially and posteriorly5
5	Pronotal collar with strong lateral carinae, forming round antero-lateral angle;
	inner orbital furrow broad, shiny, slenderly ruguloseS. murotai (Tsuneki)
_	Pronotal collar without lateral carina or carina incomplete, without antero-lateral
	angle; inner orbital furrow lacking6
6	Occipital carina complete, distinctly crenulate; scutellum with midsize sparse
	punctures, median line weakly impressed; posterior surface of propodeum with
	sturdy reticulation
_	Occipital carina incomplete, not crenulate; scutellum with fine sparse punctures,
	without median line; posterior surface of propodeum with sparse, longitudinal
	rugae or irregular rugae
7	Mesoscutum with large punctures, anterior and posterior area with dense longi-
	tudinal micro sculptures; vertex with few punctures; pronotal collar with sturdy
	incomplete anterior carinaS. interruptus sp. n.
_	Mesoscutum with tiny punctures, without micro sculpture or slightly coriaceous
	anteriorly; vertex impunctate; pronotal collar with strong complete anterior ca-
	rina
8	Dorsal surface of petiole distinctly widened toward apex; lateral surface of pro-
	podeum with contiguous, slender or sturdy, oblique rugae; admedian and parap-
	sidal line weakly impressed; median and upper frons impunctate; pygidial area
	impunctate, with dense longitudinal rugae S. convergens ami Tsuneki
_	Dorsal surface of petiole slightly widened toward apex; lateral surface of propo-
	deum reticulate; admedian and parapsidal line distinct; median and upper frons
	with fine punctures; pygidial area with two lines of large punctures, without
	rugae

Males (unknown for S. fronticoncavus sp. n. and S. interruptus sp. n.)

1	Clypeus nearly flat or flat (OR)
_	Clypeus reflected toward apex
2	Frontal furrow lacking; parapsidal line weakly impressed; vertex behind ocelli
	impunctate
_	Frontal furrow fine and weak on upper frons, anteriorly deeper, broader and dis-
	tinct; parapsidal line distinct; vertex behind ocelli with fine punctures
3	Scrobal suture inconspicuous, lacking, or just a single weak carina (PR)
_	Scrobal suture broad, distinctly crenate and complete (OR)4
4	Pronotal collar with strong lateral carinae, forming round antero-lateral angle
_	Pronotal collar without lateral carina, without antero-lateral angle5
5	Median and upper frons with punctures; vertex behind ocelli with punctures;
	propodeal enclosure U-shaped medially; dorsal surface of petiole slightly widened
	toward apex6
_	Median and upper frons impunctate; vertex behind ocelli impunctate; propodeal
	enclosure triangular medially; dorsal surface of petiole distinctly widened toward
	apex7
6	Frontal furrow weakly impressed; gena with fine punctures; admedian line weakly
	impressed; pronotal lobe white; tegula yellowish S. capoblongus sp. n
_	Frontal furrow distinctly impressed; gena with midsize punctures; admedian line
	distinctly impressed; pronotal lobe ivory; tegula dark brown
	S. japonicus Tsuneki
7	Gena finely punctate; mesoscutum with tiny punctures; admedian and parapsidal
	line weakly impressed
_	Gena impunctate; mesoscutum with large punctures; admedian and parapsidal
	line distinctly impressed

Taxonomy

Family Crabronidae Subfamily Pemphredoninae

Genus Stigmus Panzer, 1804

Type species. Stigmus pendulus Panzer, 1804, by monotypy.

Stigmus capoblongus Bashir & Ma, sp. n.

http://zoobank.org/CA9A6376-28E7-42A3-9846-78C3BB171BAE Figs 1, 6a

Type material. Holotype: 3° , China: Gansu: Dangxian: Daheba, 35°32'N, 105°17'E, 30.VII.2004, 2003m, No. 200707614, coll. Qiong Wu (ZJU); Paratypes: 33° , China: Gansu: Dangxian: Daheba, 35°32'N, 105°17'E, 30.VII.2004, 2530m, No. 200707818, 200707830, coll. Min Shi, No. 200707834, coll. Qiong Wu (ZJU); 13° , China: Shanxi: Liuba: Ziboshan, 38°19'N, 111°28'E, 2004.VIII.3, 1632m, No. 200707852, coll. Min Shi (ZJU); 13° , China: Henan: Funiushan Mount, 33°37'N, 111°43'E, 10.VII.1996, No. 973367, coll. Ping Cai (ZJU).

Diagnosis. Differs from *S. japonicus* Tsuneki (1954) by frontal furrow weakly impressed, inconspicuously; median and upper frons with fine sparse punctures; admedian line weakly impressed; lateral surface of propodeum shiny and smooth anteriorly and medially, distinctly coriaceous mixed with several longitudinal rugae posteriorly. Closely related to *S. quadriceps* Tsuneki but differs by free margin of clypeus with two triangular teeth medially; flagellomere beneath fulvous, above, remaining reddish brown to dark brown; scutellum shiny, with fine sparse punctures; petiole subquadrate (non-cylindrical); pronotal collar with strong carinae anteriorly, lateral carina lacking, without antero-lateral corner.

Description. Male (Figs 1, 6a):

Measurements. BL: 5–5.5 mm; HW : HLD : HLF = 76 : 43 : 57; HW : EWd : EW : TW : EL = 76 : 23 : 26 : 20 : 46; length of scape : length of pedicel : length of flagellomere I : width of flagellomere I : length of flagellomere II : width of flagellomere II = 21 : 8 : 9 : 3 : 8 : 3; PL : PW : LTI : WTI = 38 : 8 : 36 : 40.

Colour pattern. Clypeus with reddish brown to dark brown band subapically; mandible yellowish except reddish brown apically; palpi ivory; scape beneath ivory, above fulvous; pedicel fulvous; flagellomere beneath fulvous, above I fulvous, remaining reddish brown to dark brown; pronotal lobe white; tegula yellowish; forewing veins brown; fore leg: yellowish to fulvous except outer margin of femur somewhat brown, coxa dark brown largely; mid leg: yellowish to fulvous except outer margin of femur somewhat brown, coxa dark brown largely; hind leg: coxa apically, trochanter, base and apex of femur, tibia largely, tarsi yellowish to fulvous, remainder dark brown; petiole black; gaster dark brown, gastral sterna II–VII posteriorly bright yellow; setae on clypeus silvery and mandible yellow.

Head. Mandible bidentate apically (Fig. 1a). Clypeus nearly flat, with dense tiny punctures, setae on clypeus dense, short; free margin of clypeus slightly produced and with two triangular teeth medially, slightly reflected (Fig. 1a). Scapal hollow half mat, coriaceous, somewhat shallow, provided with a vestigial minute tubercle medially, not spined. Frontal furrow very fine and weakly impressed, inconspicuously, sometimes lacking. Median and upper frons shiny, with fine sparse punctures, gently convex.



Figure 1. *Stigmus capoblongus* Bashir & Ma, sp. n. (male). **a** Frontal view of head **b** dorsal view of head **c** dorsal view of collar **d** dorsal view of propodeum **e** dorsal view of petiole and gastral tergum I **f** lateral view of petiole and gastral tergum I **g** dorsal view of male genitalia **h** lateral view of male genitalia i ventral view of male genitalia. Scale bars: 1 mm (**a**–**f**); 1.24 mm (**g**–**i**).

Ocellar triangle area flat, shiny, impunctate, area near eyes with dense, short, impressed lines, opaque area smaller than hind ocellus. Basal half of vertex shiny, with sparse fine punctures, posterior area half mat, with inconspicuous microsculpture and fine sparse punctures (Fig. 1b). Gena shiny, with several fine punctures dorsally, ventral gena shiny and smooth. Head from above with temples slightly convergent posteriorly. Occipital carina incomplete, not ending in hypostomal carina, suddenly ended at the posterior ridge of stomal hollow, not tooth, much narrowed, no crenulate; inner and outer orbital furrows lacking; flagellomeres without tyloids, normal.

Mesosoma. Pronotal collar with strong carinae anteriorly, lateral carina lacking, without antero-lateral corner (Fig. 1c). Mesoscutum shiny, with several fine punctures, anterior area with dense large punctures medially; admedian line weakly impressed, extending to half of scutum. Prescutal sutures deeply grooved and crenulate, reaching one third of scutum. Parapsidal line distinct. Scutellum shiny, with fine sparse punctures. Metanotum slenderly coriaceous. Mesopleuron shiny, with tiny, sparse or dense punctures, posterior mesopleuron with sparse, short, sturdy, longitudinal rugae, episcrobal area with dense, fairly slender, longitudinal rugae, scrobal suture, omaulus and hypersternaulus broadened, distinctly crenate, scrobal suture complete. Propodeal enclosure U-shaped medially, and with a sturdy, longitudinal median carina and sparse transvers rugae, with several sturdy, oblique longitudinal rugae laterally (Fig. 1d). Posterior surface of propodeum with irregular rugae, groove inconspicuous. Lateral surface of propodeum shiny and smooth anteriorly and medially, distinctly coriaceous mixed with several longitudinal rugae posteriorly.

Legs. Normal, outer surface of hind tibia with three long, slender, fulvous to dark brown, spines.

Wings. Forewing venation typical for genus *Stigmus*, hindwing media diverging beyond cu-a.

Metasoma. Dorsal surface of petiole subquadrate (cross section), slightly convex and widened toward apex slightly, and with two sturdy, longitudinal median carinae, area between carinae with dense, sturdy, irregular rugae, median and posterior areas with two sturdy, longitudinal, lateral carinae on each side (Fig. 1e). Lateral surface of petiole with a few strong longitudinal carinae (Fig. 1f). Ventral surface of petiole with 4 sturdy, short, longitudinal carinae posteriorly. Gaster segments shiny, nearly impunctate. Male genitalia (Fig. 1g–i).

Female. Unknown.

Distribution. China (Gansu, Shanxi).

Etymology. The specific name, *capoblongus*, is derived from the Latin *cap*- (= head) and the Latin word *oblongus* (= oblong), referring to the oblong head.

Stigmus denticorneus Bashir & Ma, sp. n.

http://zoobank.org/D79E43E1-99E2-4D66-8B65-B2E714AE7C58 Figs 2, 6b, c

Type material. Holotype: ♀, China: Gansu: Dangxian: Daheba, 35°32'N, 105°17'E, 30.VII.2004, 2530m, No. 200707781, coll. Qiong Wu (ZJU); Paratypes: 1♀7♂, China: Gansu: Dangxian: Daheba, 35°32'N, 105°17'E, 30.VII.2004, 2530m, ♀, No. 200707788, 7♂, No. 200707785, 200707812, 200707771, 200707795, 200707816, 200707814, 200707829, coll. Qiong Wu, Min Shi (ZJU).

Diagnosis. Distinguished from *S. japonicus* by combination of characters: in female, free margin of clypeus slightly produced and with two distinct cornuted teeth medially, deeply emarginated in the middle; scrobal suture inconspicuous, just with several longitudinal rugae; lateral surface of petiole with two strong longitudinal carinae; admedian and parapsidal line weakly impressed; posterior surface of propodeum with a shallow narrow median groove, shiny, remaining with contiguous punctures and sparse irregular oblique longitudinal rugae. Closely related to *S. quadriceps* except antenna dark brown; forewing veins brown; gena with sparse midsize to large punctures dorsally; in male, frontal furrow distinctly impressed on upper frons; free margin of clypeus slightly produced and nearly truncate medially; anterior area of pronotal collar narrowly emarginated in middle, antero-lateral corner lacking; petiole subquadrate (non-cylindrical), slightly convex, not longer than 1st abdominal tergite.

Description. Female (Figs 2a–g, 6b):

Measurements. \bigcirc BL: 5 mm; HW : HLD : HLF = 68 : 42 : 52; HW : EWd : EW : TW : EL = 68 : 15 : 20 : 21 : 42; length of scape : length of pedicel : length of flagellomere I : width of flagellomere I : length of flagellomere II : width of flagellomere II = 20 : 8 : 6 : 4 : 6 : 4; PL : PW : LTI : WTI = 37 : 9 : 32 : 38. \bigcirc , BL: 3.8–4.2 mm;



Figure 2. *Stigmus denticorneus* Bashir & Ma, sp. n. (**a–g** female **h–l** male). **a**, **h** Frontal view of head **b**, **i** dorsal view of head **c** dorsal view of collar **d** dorsal view of propodeum **e** dorsal view of petiole and gastral tergum I **f** lateral view of petiole and gastral tergum I **g** dorsal view of pygidial plate **j** dorsal view of male genitalia **k** lateral view of male genitalia **l** ventral view of male genitalia. Scale bars: 1 mm (**a**, **b**, **d–f**, **h**, **i**); 1.63 mm (**c**, **g**, **j–l**).

HW : HLD : HLF = 62 : 36 : 48; HW : EWd : EW : TW : EL = 62 : 16 : 21 : 14 : 38; length of scape : length of pedicel : length of flagellomere I : width of flagellomere I : length of flagellomere II : width of flagellomere II = 15 : 7 : 6 : 3 : 7 : 3.5; PL : PW : LTI : WTI = 34 : 10 : 28 : 28.

Colour pattern. Clypeus with reddish brown to dark brown band subapically; mandible yellowish except reddish brown apically; labrum dark brown; palpi fulvous; antenna beneath fulvous and dark brown; pronotal lobe ivory; tegula fulvous; forewing veins brown; fore and mid legs: base and apex of femur, tibia, tarsi fulvous, trochanter and remaining femur dark brown; hind leg basal one fourth of tibia and tarsus fulvous, remaining tibia dark brown; petiole black; gaster dark brown; setae on clypeus and mandible yellow.

Head. Mandible tridentate apically, median tooth larger (Fig. 2a). Labrum pentagonal, apex deeply emarginated (Fig. 2a). Clypeus shiny, slightly convex, with sparse midsize punctures, setae on clypeus sparse, long; free margin of clypeus slightly produced and with two distinct cornuted teeth medially, slightly reflected (Fig. 2a). Scapal hollow half mat, coriaceous, somewhat shallow, provided with a vestigial minute tubercle medianly, not spined. Frontal furrow very fine and weakly impressed, inconspicuous. Median and upper frons shiny, with fine sparse punctures, gently convex. Ocellar triangle area flat, shiny, impunctate, near eyes area with dense, short, impressed lines, opaque area smaller than hind ocellus. Vertex behind ocelli half mat, with slender microsculpture, and fine sparse punctures. Gena shiny, with sparse midsize to large punctures dorsally (Fig. 2b), ventral gena shiny, smooth. Head from above with temples rarely convergent posteriorly, subquadrate. Occipital carina incomplete, not ending in hypostomal carina, suddenly ended at the posterior ridge of stomal hollow, not tooth, much narrowed, no crenulate; inner and outer orbital furrows lacking.

Mesosoma. Anterior area of pronotal collar with sturdy carinae (incomplete), narrowly emarginated in middle, lateral carina lacking, antero-lateral corner lacking (Fig. 2c). Mesoscutum half mat, anterior area with large dense punctures and slender coriaceous, remaining with sparse, midsize to large punctures. Admedian line weakly impressed, extending to half of scutum. Prescutal sutures deeply grooved, reaching one third of scutum. Parapsidal line weakly impressed. Scutellum shiny, with fine sparse, punctures; metanotum slenderly coriaceous. Mesopleuron shiny, with sparse, midsize punctures, episcrobal area with dense longitudinal rugae, omaulus and hypersternaulus broadened, distinctly crenate, scrobal suture inconspicuous, just with several longitudinal rugae. Propodeal enclosure elongate, U-shaped medially, and with a sturdy longitudinal median rugae and sparse transvers rugae, lateral area with contiguous, irregular rugae and punctures mixed with several, sturdy, oblique longitudinal rugae laterally (Fig. 2d). Posterior surface of propodeum with a shallow narrow median groove, shiny, remaining with contiguous punctures and sparse, irregular, oblique longitudinal rugae (Fig. 2d). Lateral surface of propodeum with slender, contiguous mixed with several sturdy, oblique longitudinal rugae.

Legs. Normal, outer surface of hind tibia with three long, slender, fulvous to dark brown, spines.

Wings. Forewing venation typical for genus *Stigmus*, hindwing media diverging beyond cu-a.

Metasoma. Dorsal surface of petiole subquadrate (cross section), slightly convex and widened toward apex slightly, with two strong longitudinal carinae, and irregular, strong rugae anteriorly and medially, lateral area with 2 strong longitudinal carinae posteriorly on each side (Fig. 2e). Lateral surface of petiole with a few strong longitudinal carinae (Fig. 2f). Ventral surface of petiole with a few strong, longitudinal carinae medially and posteriorly. Gastral segments shiny, nearly impunctate, gastral sternum VI with fine, coarse punctures, half mat. Pygidial area shiny, broadly U-shaped, apex rounded, with 2 lines, large punctures and setae medially (Fig. 2g).

Male (Figs 2h–l, 6c). Almost same to female except mandible ivory with reddish brown apically; palpi ivory; flagellomere reddish brown to dark brown; pronotal lobe white; fore and mid legs: trochanter, base and apex of femur, tibia, tarsi yellowish to fulvous, remaining dark brown; setae on clypeus dense, silvery, short. Mandible bidentate apically (Fig. 2h); clypeus near flat, with dense tiny punctures; free margin of clypeus slightly produced and nearly truncate medially, moderately reflected apically (Fig. 2h); frontal furrow distinctly impressed on upper frons; median and upper frons shiny, with several midsize to large punctures, strongly convex; ocellar triangle area slightly convex, shiny, impunctate, near eyes area with dense, short, impressed lines, opaque area large (Fig. 2i); vertex behind ocelli half mat, slenderly coriaceous, with

several shallow, midsize punctures; gena shiny, inconspicuous coriaceous, with several fine to midsize punctures dorsally; head from above with temples somewhat roundly convergent posteriorly (Fig. 2i); occipital carina incomplete, distinctly crenulate; flag-ellomeres without tyloids, normal. Male genitalia (Fig. 2j–l).

Distribution. China (Gansu).

Etymology. The specific epithetic, is derived from the Latin *dent-* (= tooth) and the Latin word *corneus* (= cornuted), referring to the free margin of clypeus with two distinct cornuted teeth medially.

Stigmus fronticoncavus Bashir & Ma, sp. n.

http://zoobank.org/C03B9D82-3729-4CD5-8D49-2A77FA164F06 Figs 3, 6d

Type material. Holotype \bigcirc , China: Yunnan: Ruili: Mengxiu, 24°05'N, 97°47'E, 2.V.1981, coll. Fasheng Li (CAU).

Diagnosis. Similar to *S. murotai* (Tsuneki, 1977) but differ by clypeus impunctate; free margin of clypeus not produced, with two small teeth medially, nearly truncate apically; labrum five lobed; ventral surface of petiole smooth, without carina; gena impunctate; parapsidal line weakly impressed; pygidial area broadened triangular shaped. *S. murotai* has the following characters: clypeus with sparse, fine punctures; free margin of clypeus narrowly produced, with two triangular teeth medially, slightly emarginated in middle; labrum trapeziform; ventral surface of petiole with dense, sturdy, short, longitudinal carinae posteriorly; gena with fine punctures; parapsidal line distinct; pygidial area broadened U-shaped.

Description. Female (Figs 3, 6d):

Measurements. BL: 5.3 mm; HW : HLD : HLF = 81 : 53 : 53; HW : EWd : EW : TW : EL = 81 : 22 : 23 : 28 : 50; length of scape : length of pedicel : length of flagellomere I : width of flagellomere I : length of flagellomere II : width of flagellomere II = 28 : 8 : 3.5 : 9 : 4; PL : PW : LTI : WTI = 34 : 8 : 40 : 43.

Colour pattern. Clypeus dark brown apically; mandible yellowish except reddish brown apically; labrum, palpi, scape, tegula and pedicel fulvous; flagellomere I–VI segments fulvous, VII-X reddish brown to dark brown; pronotal lobe yellowish; forewing veins brown; legs fulvous except coxa dark brown basally; petiole black; metasoma black, last segment dark brown; setae on clypeus and mandible golden.

Head. Mandible tridentate apically (Fig. 3a), median tooth larger, outer margin of mandible with a broad triangular tooth nearly apical area (Fig. 3b). Labrum with five lobes, apex with two lateral teeth and round teeth medially (Fig. 3a). Clypeus shiny, impunctate, fairly deeply impressed, setae on clypeus sparse, long; free margin of clypeus not produced, nearly truncate apically, and with two small teeth medially and two blunt teeth laterally, median teeth slightly reflected (Fig. 3a). Scapal hollow shiny, fairly deep and broad, not well outlined, provided with a small round tubercle medially, not spined. Frontal furrow lacking. Median and upper frons shiny, impunc-



Figure 3. *Stigmus fronticoncavus* Bashir & Ma, sp. n. (female). **a** Frontal view of head **b** ventral view of mandible **c** dorsal view of head **d** dorsal view of collar **e** dorsal view of propodeum **f** dorsal view of petiole and gastral tergum I **g** lateral view of petiole and gastral tergum I **h** dorsal view of pygidial plate. Scale bars: 1 mm (**a–h**).

tate. Ocellar triangle area flat, shiny, impunctate, near eyes area with 3 or 4 short impressed lines, opaque area small. Vertex behind ocelli shiny, impunctate; gena shiny, smooth and impunctate (Fig. 3c). Head from above with temples somewhat roundly convergent posteriorly. Occipital carina incomplete, not ending in hypostomal carina, suddenly ended at the posterior ridge of stomal hollow, forming a blunt tooth, much narrowed, not crenulate. Inner orbital furrow broad, shiny, with inner marginal carina distinct; outer orbital furrow lacking.

Mesosoma. Anterior and lateral areas of pronotal collar with strong carinae, forming blunt angle at antero-lateral corner (Fig. 3d). Mesoscutum shiny, with tiny sparse punctures. Admedian line weakly impressed, extending to half of scutum. Prescutal sutures shallowly grooved and crenulate, reaching only anterior of scutum; parapsidal line weakly impressed. Scutellum shiny, with fine sparse punctures. Metanotum slenderly rugulose. Mesopleuron with dense sparse punctures, posterior mesopleuron shiny, with several short, slender, longitudinal rugae, episcrobal area with sparse, irregular, longitudinal rugae, scrobal suture, omaulus and hypersternaulus broadened, distinctly crenate, scrobal suture complete. Propodeal enclosure triangular medially (Fig. 3e), with a sturdy longitudinal median carina and sparse transvers rugae, with sparse sturdy oblique longitudinal rugae laterally; posterior surface of propodeum with sparse irregular rugae, forming several smooth areas (Fig. 3e); lateral surface of propodeum with sparse, sturdy, oblique longitudinal rugae.

Legs. Normal, outer surface of hind tibia with three long, slender, fulvous to dark brown, spines.

Wings. Forewing venation typical for genus *Stigmus*, hindwing media diverging before cu-a.

Metasoma. Dorsal surface of petiole subquadrate (cross section), slightly convex and widened toward apex distinctly, basal half of petiole with two sturdy lateral carinae and dense irregular rugae, apex with dense, sturdy, longitudinal carinae posteriorly (Fig. 3f); lateral surface of petiole with a few strong, longitudinal carinae medially and posteriorly (Fig. 3g); ventral surface of petiole shiny, smooth, without carina. Metasomal segments shiny, nearly impunctate, gastral sternum VI with fine or coarse punctures, half mat; pygidial area shiny, broadly triangular, smooth (Fig. 3h).

Male. Unknown.

Distribution. China (Yunnan).

Etymology. The name, *fronticoncavus*, is derived from the Latin *front-* (= frons) and the Latin word *concavus* (= concave), referring to the hollow, deep and broad scapal.

Stigmus interruptus Bashir & Ma, sp. n.

http://zoobank.org/636548BE-E8B7-47D5-A59F-D71CBCC4DB21 Figs 4, 6e

Type material. Holotype \bigcirc , China: Tibet: Linzhi, 29°42'N, 87°21'E, 20.VIII.2003, No. 20035170, coll. Dejimeiduo (ZJU); Paratypes: 2 \bigcirc , same data as Holotype except No. 20035185, 20034328; 1 \bigcirc , China: Tibet: Sejilashan Mount, 29°59'N, 94°54'E, 1.IX.2002, No. 20032992, coll. Naiquan Lin (ZJU).

Diagnosis. Distinguished from closely related species *S. japonicus* by pronotal lobe white; median and upper frons with midsize punctures; vertex behind ocelli with midsize punctures; pygidial area half mat, apex truncate; lateral surface of petiole with two strong longitudinal carinae; mesoscutum with sparse large punctures; posterior surface of propodeum with a shallow somewhat narrow median groove, remaining with contiguous punctures and several oblique longitudinal rugae. *Stigmus japonicus* has following characters: pronotal lobe ivory; median and upper frons with fine punctures; vertex behind ocelli impunctate; pygidial area shiny, apex round; lateral surface of petiole with a few strong longitudinal carinae; mesoscutum with fine sparse punctures; posterior surface of propodeum with irregular rugae, groove inconspicuous.

Description. Female (Figs 4, 6e):

Measurements. BL: 4.3–4.8 mm; HW : HLD : HLF = 65 : 40 : 55; HW : EWd : EW : TW : EL = 65 : 14 : 18 : 21 : 42; length of scape : length of pedicel : length of flagellomere I : width of flagellomere I : length of flagellomere II : width of flagellomere II = 20 : 7 : 8 : 4 : 8 : 4.5; PL : PW : LTI : WTI = 34 : 9 : 34 : 36.

Colour pattern. Clypeus with reddish brown to dark brown band subapically; mandible ivory except reddish brown apically; palpi yellowish; scape beneath ivory, above dark brown largely; pedicel beneath fulvous, dark brown above; flagellomere dark brown to black; pronotal lobe white; tegula fulvous; forewing veins dark brown; fore and mid tibia, tarsi, femur (base and apex), trochanter, hind coxa, basal one third



Figure 4. *Stigmus interruptus* Bashir & Ma, sp. n. (female). **a** Frontal view of head **b** ventral view of mandible **c** dorsal view of head **d** dorsal view of collar **e** dorsal view of propodeum **f** dorsal view of petiole and gastral tergum I **g** dorsal view of pygidial plate **h** lateral view of petiole and gastral tergum I. Scale bars: 1 mm (**a**, **c**, **e**, **f**, **h**); 0.95 mm (**b**); 1.24 mm (**d**, **g**).

of hind tibia (remaining tibia dark brown) fulvous; petiole black; metasoma black except last segment reddish brown apically; setae on clypeus and mandible silvery.

Head. Mandible tridentate apically (Fig. 4a), median tooth larger (Fig. 4b). Clypeus shiny, flat, with sparse, midsize punctures, setae on clypeus sparse, long; free margin of clypeus narrowly produced and with two triangular teeth medially, slightly reflected (Fig. 4a). Scapal hollow shiny, somewhat shallow, broadened, not well outlined, without tubercle medially. Frontal furrow very fine and weakly impressed, inconspicuous. Median and upper frons shiny, with midsize sparse punctures, gently convex. Ocellar triangle area flat, shiny, impunctate, near eyes area with dense, short, impressed lines, opaque area large. Vertex behind ocelli shiny, with several midsize punctures (Fig. 4c). Gena shiny, with sparse, midsize to large punctures dorsally, ventral gena shiny and smooth. Head from above with temples somewhat roundly convergent posteriorly. Occipital carina incomplete, not ending in hypostomal carina, suddenly ended at the posterior ridge of stomal hollow, not tooth, much narrowed, no crenulate; inner and outer orbital furrows lacking.

Mesosoma. Anterior area of pronotal collar with sturdy carinae, incomplete, narrowly emarginated in middle, lateral carina lacking, without antero-lateral angle (Fig. 4d). Mesoscutum half mat, with sparse large punctures, anterior and posterior areas with dense, longitudinal micro-sculptures. Admedian line distinct, extending to half of mesoscutum. Prescutal sutures deeply grooved and crenulate, reaching half of mesoscutum. Parapsidal line distinct. Scutellum shiny, with fine sparse punctures. Metanotum slenderly coriaceous. Mesopleuron shiny, smooth, episcrobal area with dense, slender, longitudinal rugae, scrobal suture, omaulus and hypersternaulus nar-

rowed, distinctly crenate, scrobal suture complete. Propodeal enclosure elongate, U-shaped medially, and with a sturdy longitudinal median rugae and sparse irregular transvers rugae (Fig. 4e), lateral area with contiguous irregular rugae mixed with sparse, slender, oblique longitudinal rugae, laterally. Posterior surface of propodeum with somewhat narrow median groove, shiny, with several transverse rugae, remaining with contiguous punctures and several oblique longitudinal rugae (Fig. 4e); lateral surface of propodeum with contiguous punctures and slender mixed with several sturdy, oblique longitudinal rugae.

Legs. Normal, outer surface of hind tibia with three long, slender, fulvous to dark brown, spines.

Wings. Forewing venation typical for genus *Stigmus*, hindwing media diverging beyond cu-a.

Metasoma. Dorsal surface of petiole subquadrate (cross section), strongly convex and widened toward apex slightly, and with two sturdy, longitudinal median carinae, and with irregular strong rugae anteriorly and medially (Fig. 4f); lateral surface of petiole with a few strong longitudinal carinae medianly and posteriorly (Fig. 4h); ventral surface of petiole with a few strong longitudinal carinae medianly and posteriorly. Metasomal segments shiny, nearly impunctate, gastral sternum VI with fine or coarse punctures, half mat; pygidial area half mat, broadly U-shaped, apex truncate, with longitudinal micro-sculptures, basal area with several large punctures (Fig. 4g).

Male. Unknown.

Distribution. China (Tibet).

Etymology. The name, *interruptus*, is derived from the Latin word *interruptus* (= interrupt), referring to the anterior area of the pronotal collar with sturdy carinae, incomplete, narrowly emarginate in the middle.

Stigmus lobomelanicus Bashir & Ma, sp. n.

http://zoobank.org/5FB42D4C-37DE-4C6E-A152-3DDE420A0BD8 Figs 5, 6f, g

Type material. Holotype \bigcirc , China: Yunnan: Xishuangbanna: Jinghong: Yexianggu, 22°09'N, 100°52'E, 23.IX.2006, coll. Hesheng Wang (YNAU); Paratypes: 1 \bigcirc , China: Yunnan: Ruili: Nanjingli, 24°05'N, 97°47'E, 5.V.1981, coll. Fasheng Li (CAU); 1 \bigcirc , China: Yunnan: Ruili, 23°59'N, 97°37'E, 2.V.1981, No. 812489, coll. Junhua He (CAU); 1 \bigcirc , China: Yunnan: Mengla: Wangtianshu Forest Park, 22°01'N, 100°47'E, 2.V.2005, coll. Peng Wang (YNAU); 1 \bigcirc 1 \bigcirc , China: Guizhou: Luodian, 25°13'N, 105°50'E, 2–5.VI.1981, coll. Fasheng Li (CAU); 1 \bigcirc , China: Yunnan: Menghai, 22°27'N, 98°20'E, 17.V.1981, coll. Fasheng Li (CAU).

Diagnosis. Differs from *S. pendulus* by free margin of clypeus strongly produced and truncate medially, frontal furrow lacking, gena with large dense punctures, scutellum with several large punctures, pygidial area broadly triangular, with dense, slender, longitudinal striations; from *S. munakatai* Tsuneki it differs by setae on clypeus and



Figure 5. *Stigmus lobomelanicus* Bashir & Ma, sp. n. (**a–g** female **h–m** male). **a, h** Frontal view of head **b, i** dorsal view of head **c** dorsal view of collar **d** dorsal view of propodeum **e** lateral view of petiole and gastral tergum I **f** dorsal view of petiole and gastral tergum I **g** dorsal view of pygidial plate **j** ventral view of gastral tergum VIII **k** dorsal view of male genitalia **l** lateral view of male genitalia **m** ventral view of male genitalia. Scale bars: 1 mm (**a–f, h, i**); 1.63 mm (**g, j–m**).

mandible golden, upper frons with midsize to large punctures, inner orbital furrow broad, pronotal collar without antero-lateral angle, scutellum with large punctures, propodeum strongly reticulate, lateral surface with longitudinal rugae, pygidial area broadly triangular; in male, free margin of clypeus truncate medially, mandible reddish brown with black basally.

Description. Female (Figs 5a–g, 6f):

Measurements. \bigcirc BL: 5.2–6.1 mm; HW : HLD : HLF = 84 : 45 : 70; HW : EWd : EW : TW : EL = 84 : 23 : 28 : 23 : 58; length of scape : length of pedicel : length of flagellomere I : width of flagellomere I : length of flagellomere II : width of flagellomere I : 25 : 8 : 7 : 4 : 7 : 5; PL : PW : LTI : WTI = 35 : 10 : 42 : 58. \bigcirc , BL: 5.2–5.5 mm; HW : HLD : HLF = 81 : 41 : 63; HW : EWd : EW : TW : EL = 81 : 25 : 29 : 15 : 55; length of scape : length of pedicel : length of flagellomere I : width of flagellomere II : width of flagellomere I : WTI = 35 : 10 : 42 : 58. \bigcirc , BL: 25 : 29 : 15 : 55; length of scape : length of pedicel : length of flagellomere I : width of flagellomere I : width of flagellomere I : width of flagellomere I : WTI = 35 : 10 : 42 : 50.

Colour pattern. Clypeus black; mandible reddish brown to dark brown except black basally and apically; palpi dark brown; scape, pedicel, tegula and flagellomere dark brown to black; pronotal lobe black; forewing veins fulvous to dark brown; fore and mid legs: tibia, tarsi, femur (apex) reddish brown to dark brown, hind tarsus dark brown; petiole and metasoma black; setae on clypeus and mandible golden.

Head. Mandible tridentate apically, median tooth larger (Fig. 5a). Clypeus shiny, with sparse fine to midsize punctures, apex with a line, large dense punctures, strongly reflected toward apex gradually, setae on clypeus sparse, long; free margin of clypeus strongly produced and truncate medially (Fig. 5a). Scapal hollow half mat, slenderly coriaceous, somewhat shallow, without tubercle medially. Frontal furrow lacking. Median frons half mat, somewhat coriaceous, upper frons with midsize to large, sparse punctures, slightly convex. Ocellar triangle area flat, shiny, impunctate, near eyes area with dense, short, impressed lines, opaque area smaller than hind ocellus. Vertex behind ocelli shiny, with fine sparse punctures, round posteriorly; gena shiny, with sparse midsize to large punctures (Fig. 5b); ventral gena shiny, with large dense punctures mixed with several irregular rugae laterally. Head from above with temples rarely convergent posteriorly, subquadrate. Occipital carina incomplete, not ending in hypostomal carina, extending to nearly base of mandible, not tooth, outer orbital furrow much narrowed, no crenulate, on lower part somewhat broad, coarsely crenulate. Inner orbital furrow broad, shiny, slenderly rugulose; outer orbital furrow lacking.

Mesosoma. Anterior and lateral areas of pronotal collar with strong carinae, without antero-lateral angle (Fig. 5c). Mesoscutum shiny, with midsize to large punctures, anterior area slenderly coriaceous. Admedian line weakly impressed, extending to one third of scutum. Prescutal sutures deeply grooved and crenulate, reaching only anterior of scutum. Parapsidal line weakly impressed. Scutellum mat, coriaceous, with several large punctures. Metanotum distinctly rugulose. Mesopleuron shiny, with sparse large punctures, posterior mesopleuron with sparse, short, sturdy, longitudinal rugae, episcrobal area with dense reticulation, scrobal suture, omaulus and hypersternaulus much broadened, distinctly crenate, scrobal suture complete. Propodeal enclosure triangular medially, and with sturdy irregular reticulation (Fig. 5d). Posterior surface of propodeum with a fairly broadened shallow median groove, and sparse sturdy transverse rugae in groove, remaining sturdy, irregularly reticulate (Fig. 5d). Lateral surface of propodeum with dense, sturdy, oblique longitudinal rugae anteriorly and medially, and irregular reticulation posteriorly.

Legs. Normal, outer surface of hind tibia with three long, slender, fulvous to dark brown, spines.

Wings. Forewing venation typical for genus *Stigmus*, hindwing media diverging before cu-a.

Metasoma. Dorsal surface of petiole subquadrate (cross section), moderately convex and widened toward apex distinctly, and with strong irregular rugae (Fig. 5f); lateral surface of petiole shiny, with several irregular rugae and two strong lateral carinae medially and posteriorly (Fig. 5e); ventral surface of petiole with 4 sturdy, short, longitudinal carinae posteriorly. Metasomal segments shiny, with fine sparse punctures, gastral sternum VI with fine or coarse punctures, half mat; pygidial area shiny, broadly triangular, with dense, slender, longitudinal striations (Fig. 5g).

Male (Figs 5h-m, 6g). Almost same to female except mandible reddish brown with black basally, setae on clypeus dense, silvery and short; mandible bidentate api-



Figure 6. a *Stigmus capoblongus* Bashir & Ma, sp. n. (male) **b, c** *Stigmus denticorneus* Bashir & Ma, sp. n. (**b** female **c** male) **d** *Stigmus fronticoncavus* Bashir & Ma, sp. n. (female) **e** *Stigmus interruptus* Bashir & Ma, sp. n. (female) **f, g** *Stigmus lobomelanicus* Bashir & Ma, sp. n. (**f** female **g** male) **a–g** lateral view, Scale bars: 1 mm (**a–g**).

cally (Fig. 5h); clypeus moderately reflected toward apex gradually, with dense fine punctures (Fig. 5h); vertex behind ocelli impunctate (Fig. 5i); gena shiny, inconspicuous coriaceous, with several large punctures dorsally, ventral gena shiny, with sturdy, sparse, irregular rugae laterally; head from above with temples distinctly convergent posteriorly; flagellomeres without tyloids, normal; dorsal surface of petiole subquadrate (cross section), slightly convex and widened toward apex slightly, and with strong irregular rugae; metasomal segments shiny, nearly impunctate. Sternum VIII (Fig. 5j). Male genitalia (Fig. 5k–m).

Distribution. China (Yunnan, Guizhou).

Etymology. The name, *lobomelanicus*, is derived from the Greek *lob-* (= lobe) and the Greek word *melanicus* (= black), referring to pronotal lobe black.

Acknowledgements

We are indebted to Dr. Xue-xin Chen (Zhejiang University, Hangzhou) and Dr. Wanzhi Cai (China Agricultural University, Beijing) for providing specimens and Dr. Wojciech J. Pulawski for giving literatures. The authors thank three reviewers P. Girish Kumar, H. Dollfuss and M.V. Mokrousov for their informative critiques which helped the improvement of the manuscript. This study was funded by the National Natural Science Foundation of China (31750002, 31760641).

References

- Allen GW (1987) *Stigmus pendulus* Panzer (Hymenoptera, Sphecidae) new to Britain. Entomologist's Gazette 38: 214.
- Bohart RM, Menke AS (1976) Sphecid wasps of the world, a genetic revision. University of California Press, Berkeley, Los Angeles, London, 695 pp. https://archive.org/details/bub_ gb_FExMjuRhjpIC
- Budrys ER (1987) Digger wasps of the genus Stigmus Panzer and Carinostigmus Tsuneki (Hymenoptera, Sphecidae) of the Far East of USSR. In: Lehr PA, Storozheva NA (Eds) New data on insect systematic of Russian Far East. DVO AN SSSR, Vladivostok. 49–56. http:// researcharchive.calacademy.org/research/entomology/Entomology_Resources/Hymenoptera/sphecidae/copies/Budrys_1987.pdf
- Budrys ER (1995) Subfamily Pemphredoninae. In: Lehr PA (Ed.) Key to the insects of Russian Far East. Vol. 4. Nauka, Sankt-Peterburg. 388–406. https://www.nhbs.com/3/series/keysto-the-insects-of-the-russian-far-east?qtview=122918
- Finnamore AT (1995) Revision of the world genera of the subtribe Stigmina (Hymenoptera: Apoidea: Sphecidae: Pemphredoninae), Part 1. Journal of Hymenoptera Research 4: 204– 284. http://biodiversitylibrary.org/page/3387491

- Jones RA (2001) Stigmus pendulus (Panzer) (Hymenoptera: Sphecidae) associated with ancient woodlands in south-east London. British Journal of Entomology and Natural History 13: 213–214. https://biodiversitylibrary.org/page/39462229
- Kolesnikov VA (1977) Sphecid wasps (Hymenoptera, Sphecidae) of the Bryansk region and their role as entomophagous insects. Entomologicheskoye Obozreniye 56: 315–325. https://eurekamag.com/research/006/462/006462410.php
- Krombein KV (1973) Notes on North American Stigmus Panzer. Proceedings of the Biological Society of Washington 86: 211–230. http://biostor.org/cache/pdf/ea/b1/26/ eab1262084380709a0d036dc2ba734aa.pdf
- Mokrousov MV (2017) To the knowledge of digger wasps of subfamily Pemphredoninae (Hymenoptera: Crabronidae) of Russia. Far Eastern Entomologist 337: 1–16. https://doi. org/10.25221/fee.337.1
- Morawitz A (1864) Verzeichniss der um St. Petersburg aufgefundenen Crabroninen. Bulletin de l'Académie Impériale des Sciences de St. Pétersbourg 7: 451–465. https://biodiversitylibrary.org/page/33683794
- Panzer GWF (1804) Faunae insectorum germanicae initiae oder Deutschlands Insecten. Felseckersche Buchhandlung, Nürnberg, Heft 86, 24 plates. https://biodiversitylibrary. org/page/15488140
- Pulawski WJ (2018) Stigmus: Catalog of Sphecidae http://researcharchive.calacademy.org/research/entomology/Entomology_Resources/Hymenoptera/sphecidae/Genera/Stigmus.pdf
- Tsuneki K (1954) The genus Stigmus Panzer of Europe and Asia, with description of eight new species (Hymenoptera, Sphecidae). Memoirs of the Faculty of Liberal Arts, Fukui University. Series II, Natural Science 3: 1–38. http://researcharchive.calacademy.org./research/ entomology/Entomology_Resources/Hymenoptera/sphecidae/copies/Tsuneki_1954a.pdf
- Tsuneki K (1977) Further notes and descriptions on some Formosan Sphecidae (Hymenoptera). Special Publications of the Japan Hymenopterists Association 2: 1–32.
- Uffen RWJ (1997) Exhibit of *S. pendulus* from Welwyn, at BENHS meeting 8 October 1996. British Journal of Entomology and Natural History 10: 181. https://biodiversitylibrary. org/page/36266245
- Uffen RWJ (1998) Exhibit of S. pendulus from Tyttenhanger, at BENHS Annual Exhibition 2 November 1996. British Journal of Entomology and Natural History 10: 181. https:// biodiversitylibrary.org/page/36266245
- Valkeila E (1956) A note on the taxonomy and nomenclature of two European species of the genus *Stigmus* Panzer. Annales Entomologici Fennici 22: 165–167.

RESEARCH ARTICLE



Reef-associated fishes from the offshore reefs of western Campeche Bank, Mexico, with a discussion of mangroves and seagrass beds as nursery habitats

D. Ross Robertson¹, Omar Domínguez-Dominguez², Yareli Margarita López Aroyo², Rigoberto Moreno Mendoza³, Nuno Simões^{3,4,5}

I Smithsonian Tropical Research Institute, Balboa, Panamá 2 Laboratorio de Biologia Acuatica, Facultad de Biologia, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacan, Mexico 3 Unidad Multidisciplinaria de Docencia e Investigación Sisal (UMDI-SISAL), Facultad de Ciencias, Universidad Nacional Autónoma de México, Puerto de Abrigo s/n, Sisal, CP 97356 Yucatán, Mexico 4 International Chair for Coastal and Marine Studies, Harte Research Institute for Gulf of Mexico Studies, Texas A and M University – Corpus Christi, Texas, USA 5 Laboratorio Nacional de Resiliencia Costera, Laboratorios Nacionales, CONACYT, Mexico

Corresponding author: D. Ross Robertson (drr@stri.org)

Academic editor: <i>Kyle Piller</i>	Received 14 February 2019	Accepted 29 March 2019	Published 9 May 2019
http	v://zoobank.org/CC93CC69-4682-	-4B45-8504-4C354B694C22	

Citation: Robertson DR, Domínguez-Dominguez O, Aroyo YML, Mendoza RM, Simóes N (2019) Reef-associated fishes from the offshore reefs of western Campeche Bank, Mexico, with a discussion of mangroves and seagrass beds as nursery habitats. ZooKeys 843: 71–115. https://doi.org/10.3897/zooKeys.843.33873

Abstract

A series of small emergent coral reefs and shallow, submerged coralliferous banks are scattered along the western edge of Campeche Bank (southwest Gulf of Mexico), 150–200 km offshore from the Yucatán Peninsula, Mexico. Here a reasonably comprehensive, annotated checklist of reef-associated fishes for one reef, Cayo Arcas (expanded from 162 to 209 species) is presented, with preliminary checklists of such fishes from three other emergent reefs (Cayo Arenas, Triángulo Oeste, Triángulo Este) and four submerged bank reefs (Banco Obispo Norte, Banco Obispo Sur, Banco Nuevo and Banco Pera). During 2017–18 a total of 260 species was observed or collected from those reefs, and previous studies and georeferenced museum records in the global aggregator Fishnet2 added another 101 shallow-living species recorded on or adjacent to those reefs. Some coral-reef fishes are thought to be strongly dependent on seagrass and mangrove areas as nursery habitats for maintenance of their local populations on reefs near to those habitats. The abundance of a number of such "nursery" species on these Campeche reefs indicates otherwise,

as there are no seagrass- or mangrove habitats for reef fishes within ~ 150 km of the study reefs. Other isolated Caribbean-area reefs that lack mangroves and, in some cases, seagrasses, also support many such nursery species of reef-fishes.

Keywords

endemic species; invasive species juvenile habitats; reef-fishes; Southwest Gulf of Mexico

Introduction

The southwest Gulf of Mexico has relatively few coral reefs, most of which are quite small. Only a few of these are offshore reefs on the broad, shallow Campeche Bank that extends 200+ km north from the Yucatán Peninsula. This part of the Gulf of Mexico has a different marine environment from the rest of that gulf (Belanger et al. 2012, Lorda et al. 2019). Due in part to the number of endemic reef-fishes found there, the shore-fish fauna of this area forms a discrete biogeographic subunit within one of three major biogeographic subdivisions of the shore-fish fauna of the Greater Caribbean (Robertson and Cramer 2014).

The reef-fish faunas of most of the Campeche Bank offshore reefs have not been documented. Only three of them have substantial published checklists: Alacranes Reef, a large (~ 300 km²) emergent reef in the center of the bank and the largest reef in the region (Gónzalez-Gándara and Arias-González 2001), Madagascar Reef, a tiny (~ 0.25 km²), shallow, submerged coralliferous rocky bank ~ 40 km offshore from Sisal, on the northwest coast of the Yucatán peninsula (Zarco-Perelló et al. 2014, Robertson et al. 2016a), and Cayo Arcas, a cluster of three small emergent reefs located near the outer edge of the southwest corner of Campeche Bank (Robertson et al. 2016b).

Here we present an expanded list of non-cryptic and cryptic reef-fishes we observed and collected at Cayo Arcas, and at seven other reefs and submerged banks (Cayo Arenas, Triángulo Oeste, Triángulo Este, Obispo Norte, Obispo Sur, Banco Nuevo and Banco Pera), scattered along the western edge of Campeche Bank, ~ 150 km from the mainland coast during 2017–18. In addition we include a list of fishes that were collected from the vicinity of those reefs and are lodged in the database of the aggregator website Fishnet2 (http://www.fishnet2.net/) by some of the 75 international museums that supply data to that website.

Surveys of local reef-fish faunas serve several purposes. They provide the grist for studies of the biogeography of reef fishes by fleshing out information on the distributions of species. If sites are small and depauperate in habitat diversity their faunal composition provides information that helps identify the importance of different habitats and reef-size for maintaining local populations of different species. Both types of information are useful for indicating the importance of sites for management and conservation purposes. Hence the reef-fish faunas of the reefs we discuss here also are of interest not only because of their location, but also because those reefs are small, isolated and lack two major ancillary habitats that are commonly found adjacent to reefs and used by reef-fishes in other parts of the Greater Caribbean: seagrass beds and mangroves.
Methods

Study reefs

The set of eight study reefs is spread from the Cayo Arcas complex in the southwest corner of Campeche Bank, to the Cayo Arenas complex, 220 km northeast of Cayo Arcas, at the northwest corner of that Bank (Figure 1). Cayo Arenas (Suppl. material 1: Figures S1–S3) is at 22.11°N, 91.39°W, Triángulo Oeste (Suppl. material 1: Figure S4) at 20.96°N, 92.3°W, Triángulo Este (Suppl. material 1: Figure S5) at 20.91°N, 92.22°W, Banco Obispo Norte (Suppl. material 1: Figure S6) at 20.49°N, 92.20°W, Banco Obispo Sur (Suppl. material 1: Figure S7a,b) at 20.41°N, 92.22°W, Banco Nuevo at 20.55°N, 91.88°W, Banco Pera (Suppl. material 1: Figure S8) at 20.73°N, 91.93°W, and Cayo Arcas (Suppl. material 1: Figures S9, S10) at 20.20°N, 91.97°W. The study reefs include all the emergent reefs on the western edge of Campeche Bank except Cayo Nuevo (21.83°N, 92.09°W), which is located ~ 95 km north of Triángulo Oeste and ~ 78 km southwest of Cayo Arenas, and all the named submerged coralliferous banks except Bancos Ingleses, ~ 15 km east-southeast of Cayo Nuevo. Cayo Arenas and Cayo Arcas each have a manned lighthouse and are permanently staffed by a lighthouse keeper and Mexican Armada marines.

Reef-fish habitats on the study reefs:

Cayo Arenas, Cayo Arcas and the two Triángulo reefs (Oeste and Este) are emergent reefs or reef complexes, with well-developed coral cover, and coral zonation patterns (Tunnell et al. 2007) similar to those of other reefs on the outer parts of the continental shelf elsewhere in the Greater Caribbean. The reef systems of Cayos Arcas and Arenas each comprise a cluster of three separate emergent reefs spread over an area of $\sim 5 \text{ km}^2$. Triángulo Oeste is a single reef with an emergent area of <0.25 km², and Triángulo Este (also known as Triángulo Este-Sur) is composed of a 5 km long line of four elongate, narrow (0.5 km wide) emergent reefs separated from each other by shallow-water distances of < 1 km (Suppl. material 1: Fig S3). Reef development on those reefs extends down to 25–30 m (Logan et al. 1969, Tunnell et al. 2007). The two Obispo banks and Banco Nuevo and Banco Pera are rocky banks that rise to within 10 m (Obispos) and - 15 m (Nuevo and Pera) of the surface. While a few small patch reefs on those banks have well developed coral cover, for the most part the surface of the areas of those banks we visited comprised rock, with a thin covering of sand and an abundance of 2–3 m high, tree-like gorgonians, with only small scattered clumps of hard corals 1 m or so in diameter, and numerous large barrel sponges. Logan et al. (1969) described the general geological and morphological characteristics of reefs, submerged coralliferous banks and inter-reef soft bottoms on the Yucatán Peninsular, and Chávez et al. (2007) summarized information about reef morphology and coral zonation patterns of Cayo Arcas. Various aspects of the habitat structure and benthic organisms found on the reefs at Cayo Arcas, Cayo Arenas and the Triángulos reefs also are described and discussed in Tunnell et al. (2007).



Figure 1. General location of study reefs on Campeche Bank. Base map by NASA.

Mangroves and seagrasses on the Campeche Bank reefs

Mangroves and beds of seagrasses (typically *Thalassia testudinum* Banks ex Koenig, 1805) represent major ancillary habitats adjacent to or within many reefs in the tropical northwest Atlantic. Those two habitats are used by many reef fishes, often as nursery habitats (Nagelkerken et al. 2017). Flores (1992), who is cited as the source of information on mangroves and seagrasses (*T. testudinum*) on Campeche Bank offshore cays by Gulfbase (http://www.gulfbase.org/checklist/pdfs/marine-spp-list.pdf) an aggregator of biological information on the Gulf of Mexico, listed mangroves as being present at Cayo Arcas but not Cayo Arcas. Flores (1992) figure 47 of the distribution of plants on the lighthouse cay at Cayo Arcas shows a few mangrove plants where currently there is a shallow (<1 m deep) pond immediately along the east and southeast side of that cay, inshore from the intertidal reef crest, but he presented no information

about their size or abundance. We noticed no mangroves in that area in 2016, but did see several small, young plants in the southeast section of the pond in 2018 (Suppl. material 1: Figure S10). Tunnell and Chapman (2001) surveyed seabird rookeries on Cayo Arenas, Cayo Arcas and Cayo Triángulo Oeste and noted vegetation on those islands, but did not mention mangroves at any of them. We saw mangroves only at Isla Arenas, in 2017. At that site there was a small (~ 30 m diameter) patch of small (up to ~ 1 m high) mangroves with slender (up to several cm diameter) trunks growing on a bottom surfaced entirely with flattened coralline rock chips in the intertidal zone on the southwest side of the Lighthouse island, on the seaward side of a saltwater pond (see Suppl. material 1: Figure S2). At low tides during our stay there (May 2017) those mangroves were completely exposed, with only small (to ~ 25 cm wide), shallow (<2 cm deep) scattered puddles containing water in the mangrove area, a few of which contained a few small gobies (Bathygobius sp.), but no other fishes (Suppl. material 1: Figure S3). Hence that mangrove patch does not represent permanently available habitat for reef fishes and would offer little shelter even at high tide. It does not constitute a patch of permanently immersed mangrove nursery habitat of the type commonly used by reef fishes. The situation vis a vis the presence of small stands of stunted, sparsely scattered mangroves on the small, low sandy cays of Campeche Bank on which intertidal habitats are quite likely to change in response to storms may well have changed at Cayo Arenas and Cayo Arcas in 25+ years since Flores' (1992) research. Tunnell et al. (2007) noted the disappearance of small stands of mangroves growing in small, beach-front ponds next to two sand cays at Alacranes Reef between the 1960s and 2000s. They also noted the presence of a small stand of mangroves growing in a pond at the southeast corner of Perez Island at Alacranes reef. That ~ 0.1 ha stand, much of which was growing on dry land around the pond, was still present in 2016 during the visit by DRR. That pond was separated from the shore by a beach berm, and only intermittently connected to the sea. As with the Cayo Arenas mangrove patch, that on Isla Perez likely does not represent a significant amount of habitat useable as a reef-fish nursery.

There are seven seagrasses in the Gulf of Mexico (Littler and Littler 2000, Green and Short 2003). Three of them, Turtlegrass, *Thalassia testudinum*; Manatee grass, *Syringodium filiforme* Kutzing in Hohenacker, 1860; and Shoal grass, *Halodule wrightii* Ascher, 1868, grow in beds that can be sufficiently dense to provide a shelter-rich habitat useable by reef-associated fishes. No live seagrasses growing on sandy bottoms were seen by us or any other divers from UNAM-Sisal studying shallow water organisms during expeditions to the study reefs in 2016–2018. Those dive sites included lagoonal areas on the leeward sides of emergent reefs and large sand patches on the submerged banks. At Cayo Arcas and Cayo Arenas the cays have shallow (<1m deep) saline ponds bordering the islands that become isolated at low tide; we saw no seagrasses growing in those. We did see substantial amounts of dead seagrass leaves deposited on the beaches of Cayo Arcas in 2016, with much smaller amounts on those beaches in 2018. However, the beaches of Cayo Arenas and the cay at Triángulo Oeste only contained windrows of dead macroalgae. The seagrass windrows on Cayo Arcas were composed of slender, cylindrical, thread-like leaves of *Syringodium* and/or *Halodule*, and no dead blades of *Thalassia* were observed. All those dead seagrass threads were either brown or bleached white, short (mostly <10cm long) and lacked leaf bases with roots attached to them. Similar threads were observed floating in the open sea near Cayo Arcas. Those three species of seagrass are restricted to shallow water in sheltered habitat with finesand and mud bottoms: the depth limit of *T. testudinum* is ~ 20m, of *S. filiforme* 25 m, and *H. wrightii* 5 m (Littler and Littler 2000; Short et al. 2010a, b, c). Robertson et al. (2016b) thought that *H. wrightii* might be growing in shallow beach-side ponds of Cayo Arcas. That does not appear to be the case. Thus it is very doubtful that any seagrasses are growing around or very near to the study reefs but missed during our expeditions between 2016 and 2018 as the emergent reefs provide the only sheltered soft substrata in their leeward lagoons, and water around the reefs is deeper than that in which these seagrasses are known to grow.

Turtlegrass was the only seagrass listed by Flores (1992) as present on offshore Campeche reefs, and he indicated it was present at Cayo Arcas, Cayo Arenas, and Cayo Triángulo (i.e., Triángulo Oeste). However, a map (map XIII) of seagrass distribution in the Gulf of Mexico by Green and Short (2003) shows them present inshore along the entire Gulf coast of the Yucatán peninsula and at Alacranes Reef, but nowhere else on Campeche Bank. It seems less likely that seagrasses, which typically grow in sheltered (e.g., lagoonal) habitats, such as that at Alacranes reef, would have vanished from our study reefs. Chávez et al. (2007) noted the absence of seagrasses on "most" Campeche reefs other than Alacranes, which they attributed to a lack of accumulation of fine sediment needed for seagrass establishment. The simplest explanation for the occurrence of the long-dead manatee/shoal grass threads on the beach of Cayo Arcas and floating in water nearby is that they drifted ~ 150 km in from grass beds along the mainland coast. Hence we conclude that two major ancillary habitats, mangroves, and seagrass beds, used by reef fishes throughout much of the wider Caribbean area currently are lacking within ~ 150 km of the offshore reefs of western Campeche Bank.

Data collection

Cayo Arenas was visited by a group of divers, including DRR, who camped on the island from 22 to 27 May, 2017. During that visit DRR made 14 dives between 0–30 m at different sites on the three reefs that comprise that reef system. During September 8–15, 2017 a group of divers on a live-aboard diving-support vessel, the 30 m long "Barco Isla Mujeres" (see https://www.youtube.com/watch?v=xt-aP0zOFTw.), visited six reefs and banks located between Cayo Arcas and Cayo Arenas. During that expedition DRR, OD-D and RMM made a total of 60 person dives, at Triángulo Oeste (September 8–10, six dives per person between 1–25 m), Triángulo Este (September 11–12; five dives per person between 1–28 m), Banco Obispo Norte (September 13, three dives per person at 9–24m), Banco Obispo Sur (September 14, three dives each at 9–25 m), Banco Nuevo (September 15, two dives each at 18–20m) and Banco Pera (September 15, one dive each at 24 m). During 19–26 June 2018 DRR, RMM and OD-D camped as part of a group of researchers from UNAM-Sisal on Cayo Arcas. Together with two assistants they made a total of 105 person dives at 17 sites on the three reefs that make up that complex. During his dives at the different reefs DRR focused on obtaining a seascape view of the fish fauna, covering large areas and noting the occurrence and abundance of non-cryptic species at different sites. The other divers on the September 2017 and June 2018 trips focused on collecting cryptic fishes using the anesthetic clove oil (10% clove oil in 70% ethanol), and non-cryptic fishes by spearing with multi-pronged pole spears. Collections with clove oil were made in two ways: the anesthetic sprayed into holes without knowing what fishes were inside, and, in other cases, after noticing suitable specimens in holes. Abundance categories given here are the same as those reported in Robertson et al. (2016b) for earlier, similar observations at Cayo Arcas: Rare (1 seen during entire expedition); Uncommon (< 5 total); Occasional (~ 20 total, at multiple dive sites); Common, widespread (scores, at most/all dive sites); Locally common (scores to hundreds at 1–2 dive sites); Abundant, widespread (hundreds to thousands at most/all dive sites).

In addition a search was made on Fishnet2 (www.fishnet2.net; accessed October 5, 2018), for records of fish species collected in two quadrants, one that encompassed Cayo Arenas and adjacent areas on its east and west sides highlighted by Google Earth (quadrat sides: 22.0°N to 22.15°N, 91.05°W to 91.55°W, ~ 885 km²), and another that encompassed all the remaining study reefs (quadrat sides: 20.05°N to 21.0°N, 91.5°W to 92.5°W; ~ 11,000 km²). We used those quadrats in part to accommodate lack of precision in georeferencing of collection records that might relate to those reefs. We incorporated Fishnet2 records of fish species that could be encountered in shallow reef habitats (< 30 m depth) or occur in pelagic and soft-bottom habitats shallower than 30m adjacent to reefs.

Tissue samples (for genetic analyses) of large, easily recognizable species of reeffishes and voucher specimens of all small cryptic species that were collected at the study reefs and preserved in ethanol have been deposited in the Ichthyological Collection of the Laboratorio de Biología Acuática, Universidad Michoacana de San Nicolás de Hidalgo, México (SEMARNAT registration number MICH-PEC-227-07-09).

Results

Table 1 includes a list of 364 fish species from 75 families now known from the west Campeche offshore reefs. Of those 360 are bony fishes, which include 260 species that we observed or collected on the study reefs between 2016–2018. In addition there are nine other species that were observed or collected on those reefs by Chávez (1966) and by Garduño (1988) but not seen by us, and museum records of 136 species in the two quadrats, 96 of which were not recorded by us on the reefs. The 136 include 48 softbottom species (46 of which we did not record on the reefs), 31 pelagic species (20 not recorded by us), and 57 species that occur on hard reef substrata (as well as other substrata in some cases), 30 of them not recorded by us. Robertson et al. (2016b) reported a fauna of 162 species from Cayo Arcas; our 2016–18 sampling increased that to 209 species, primarily as a result of collection of 35 cryptic species using clove-oil anesthetic.

cted	
colle	
fishes	
water	
llow v	
of sha	
ecies o	
of spo	
cords	
ım re	
muser	
i do bi	
nk, ar	
he Ba	
mpec	
of Ca	
edge	
stern	
the we	
s on 1	
8 reef	
ed on	
ollecte	e reefs
and c	those
rved	orate
s obse	ncorp
f fishe	that i
List of	ıdrats
e I .]	ro quá
0	×

			·				6					
Taxon Name	Species Habitat	Triángulo Oeste	l'riángulo Este	Ubispo Norte	Obispo Sur	Banco Nuevo	Banco Pera	Arenas	Arcas 2016–18	No. reefs	Arenas quadrat	Arcas quadrat
GINGLYMOSTOMATIDAE												4
Ginglymostoma cirratum	R&SB	R	R	R				R		4		Ρ
CARCHARHINIDAE												
Carcharhinus brevipinna	Ρ		R	R						2		
Carcharhinus limbatus p	Р							C ⁶⁶		1		
Carcharhinus perezii	Ρ							R		1		
SPHYRNIDAE												
Sphyrna lewini	Р							R		1		
KAJIDAE												
Rostroraja texana	SB											Р
UROTRYGONIDAE												
Urobatis jamaicensis * p	SB				R				R	2		
DASYATIDAE												
Hypanus americanus p AETOBATIDAE	SB			R	R				U	3		
Aetobatus narinari p	SB							R	Ь	2		
MEGALOPIDAE												
Megalops atlanticus p AI RIII IDAF	Р	D						U	IC	3		
Albula vulves	SB											Ъ
MURAENIDAE												
Echidna catenata *	C,R								P^{2018}	1		
Enchelycore carychroa *	C,R	Ъ							P^{2018}	2		
Enchelycore nigricans p	C,R	Ъ				Ρ		C ⁶⁶		3		
Gymnothorax funebris * p	SC,R	C ⁶⁶						$P G^{ss}$		2		
Gymnothorax miliaris *	C,R	Ъ	Ъ					Ъ		С		
Gymnothorax moringa p	SC,R	C ⁶⁶	Ρ	Р				C ⁶⁶	Р	2		
Gymnothorax nigromarginatus	SB											Ρ
Gymnothorax vicinus	C,R				Р					1		

Taxon Name	Species Habitat	Triángulo Oeste	Triángulo Este	Obispo Norte	Obispo Sur	Banco Nuevo	Banco Pera	Arenas	Arcas 2016–18	No. reefs	Arenas quadrat	Arcas quadrat
OPHICHTHIDAE												
Ahlia egmontis	SB,C										Ъ	Ρ
Myrophis platyrhynchus	SB,C											Ρ
ENGRAULIDAE												
Anchoviella perfasciata	Р											Ρ
Engraulis eurystole	Ρ											Ρ
CLUPEIDAE												
Etrumeus acuminatus	Р											Ъ
Jenkinsia lamprotaenia p	Р							Α	А	2		Р
Opisthonema oglinum *	Р								P^{2018}	1		Р
Sardinella aurita	Ъ											Ρ
SYNODONTIDAE												
Synodus foetens	SB											Ρ
Synodus intermedius	SB,R		R					R		2		Ρ
Synodus poeyi	SB											Ρ
Synodus synodus *	SB,R								R^{2018}	1		
Trachinocephalus myops	SB											Ρ
OPHIDIIDAE												
Brotula barbata	С											Р
Lepophidium brevibarbe	SB,C											Ρ
DINEMATICHTHYIDAE												
Ogilbia cayorum * p BATRACHOIDIDAE	R,C	Ъ	Ъ	Ъ	Р			Cé		Ś		
Porichthys plectrodon ANTENNARIIDAE	SB											Р
Antennarius scaber	C,R											Ь
	ę											ţ
Halieutichthys aculeatus	SB											Ъ
Halieutichthys bispinosus	SB											Ъ
Ogcocephalus corniger	SB											Ъ
Ogcocephalus cubifrons	SB											Ρ
Ogcocephalus parvus	SB											Р

Taxon Name	Species Habitat	Triángulo Oeste	Triángulo Este	Obispo Norte	Obispo Sur	Banco Nuevo	Banco Pera	Arenas	Arcas 2016–18	No. reefs	Arenas quadrat	Arcas quadrat
ATHERINIDAE											I	
Atherina harringtonensis * p	Р		IC						А	2		
Atherinomorus stipes p	Р	C ⁶⁶						LA	А	3		Ρ
EXOCOETIDAE												
Cheilopogon cyanopterus	Ρ											Ρ
Cheilopogon heterurus	Ρ											Ρ
Parexocoetus brachypterus hrachynterus	Р											Р
Parexocoetus hillianus *	Ρ			Ρ	Ρ					2		Ρ
HEMIRAMPHIDAE												
Euleptorhamphus velox	Р											Р
Hemiramphus brasiliensis	Ρ											Ρ
Hyporhamphus unifasciatus	Ъ											Р
DELUNIDAE												
Ablennes hians	Ρ											Ъ
Platybelone argalus argalus *	Р		Ρ							1		Ъ
Tylosurus acus acus	Р											Р
Strongylura notata p	Р							G"		1		
HOLOCENTRIDAE												
Neoniphon marianus p	R,SC	R						UC G*		2		
Holocentrus adscensionis p	R			0			Р	C	U	4		Ρ
Holocentrus rufus * p	R	0	LC	0	0	Р	Ъ	$\mathbb{C} \mathbf{G}^{ss}$	0	8		Ρ
Myripristis jacobus * p	R							0	U	2		
Neoniphon coruscum	R,SC					Ρ				1		
Neoniphon vexillarium * p	R,SC	C ⁶⁶				Ъ		C	N	4		
Plectrypops retrospinis p	R,C							Cee		1		
	(F								5 018			
AULOSTOMIDAE	R,C									I		
Aulostomus maculatus *p	R	0	0	0	0	Р	Р	$0 G^{ss}$	N	8		
FISTULARIIDAE												
Fistularia tabacaria	R,SB											Ъ

Taxon Name	Species Habitat	Triángulo Oeste	Triángulo Este	Obispo Norte	Obispo Sur	Banco Nuevo	Banco Pera	Arenas	Arcas 2016–18	No. reefs	Arenas quadrat	Arcas quadrat
DACTYLOPTERIDAE											I	I
Dactylopterus volitans	SB											Р
SCORPAENIDAE												
Pterois volitans * p	R	R	UC		Ŋ			D	0	2		
Scorpaena brasiliensis	R,SC											Р
Scorpaena calcarata	R,SC											Р
Scorpaena dispar	R,C											Ъ
Scorpaena plumieri p	R,SC	C ⁶⁶								1		Р
Scorpaenodes caribbaeus *	R,C								P^{2018}	1		
Scorpaenodes tredecimspinosus *	R,C								P^{2018}	1		
TRIGLIDAE												
Prionotus ophryas	SB											Р
Prionotus punctatus	SB											Р
Prionatus raseus	SB											Р
Prionotus rubio	SB											Р
Prionotus stearnsi	SB										Р	Р
EPINEPHELIDAE												
<i>Cephalopholis cruentata</i> * p	R	C	С	U	C	C		C G*	С	7		
<i>Cephalopholis fulva</i> p	R		R					G	R	3		Ъ
<i>Cephalopholis furcifer</i> * p	Ъ	C	D					LC	C	4		Р
Epinephelus adscensionis *p	R	R	0	0	0	Ŋ	Ъ	0	C	8		Р
Epinephelus guttatus * p	R	D	0	0	0	R	Ъ	0	C	8		Ъ
<i>Epinephelus itajara</i> p	R							C ⁶⁶		1		
Epinephelus morio *	R,SB			1						1		
Epinephelus striatus p	R	R						C ⁶⁶ G ⁸⁸		2		
Hyporthodus flavolimbatus	R,SB										Р	
Hyporthodus niveatus	R,SB											Р
Mycteroperca acutirostris *	R			R						1		
Mycteroperca bonaci p	R		R					C ⁶⁶	С	3		Р
Mycteroperca interstitialis p	R	0	0	0	Ŋ	0		0	LC	7		
Mycteroperca microlepis p	R								Ŋ	1		
Mycteroperca phenax p	R								N	1		Р
Mycteroperca tigris p	R	Cee						C ⁶⁶	C	3		

Taxon Name	Species Habitat	Triángulo Oeste	Triángulo Este	Obispo Norte	Obispo Sur	Banco Nuevo	Banco Pera	Arenas	Arcas 2016–18	No. reefs	Arenas quadrat	Arcas quadrat
Mycteroperca venenosa	R	Я	n		D			0	R ²⁰¹⁸	5	1	1
SERRANIDAE												
Centropristis ocyurus	SB											Р
Diplectrum bivittatum p	SB							R		1		Ρ
Diplectrum formosum	SB											Р
Hypoplectrus aberrans * p	R	R	0	D	N		Ρ	D	LC	7		
Hypoplectrus ecosur * p	R		R	R		0	0		LC	2		
Hypoplectrus floridae *	R								R^{2018}	1		
Hypoplectrus gemma * p	R	0	0	D		D		D	R	9		
Hypoplectrus guttavarius p	R							C ⁶⁶		1		
Hypoplectrus indigo * p	R	R	R						Ŋ	3		
Hypoplectrus maculiferus p	R		R						R	2		
Hypoplectrus nigricans * p	R		R	R		R			0	4		
Hypoplectrus puella * p	R	0	0	0		0	Ρ	U	0	7		
Hypoplectrus randallorum * p	R	R	Ŋ	R					R	4		
Hypoplectrus unicolor * p	R	R	0					R	R	4		
Pseudogramma gregoryi *	C,R			Ъ					P^{2018}	2		
Rypticus bistrispinus	U											Ρ
Serranus baldwini * p	R			D	0				R	3		
Serranus tabacarius * p	R			LC	0			D	LC	4		
Serranus tigrinus * p	R	0	0	0	0			U	U	9		
Serranus tortugarum * p GRAMMATIDAE	R	LC	LC		0	0		LC	IC	9	Ъ	
Gramma loreto * p	R	U	C	C	C		R	LC	C	7		
OPISTOGNATHIDAE												
Lonchopisthus micrognathus	SB,C											Ъ
<i>Opistognathus aurifrons</i> * p	SB		LC	R	0	0	Ρ	LC	LC	7		
Opistognathus macrognathus * PRIACANTHIDAE	SB,C								P^{2018}	1		
Heteropriacanthus cruentatus p	R,SC							R		1	Р	
Priacanthus arenatus	R											Ъ
APOGONIDAE												
Apogon aurolineatus p	C,R							Ъ		1		

	•	ŀ	-	. 10	. 10	-	-					
Taxon Name	opecies Habitat	Oeste	Este	Norte	Sur	Danco Nuevo	Pera	Arenas	AICas 2016–18	No. reefs	Arenas quadrat	Arcas quadrat
Apogon binotatus *	C,R	Ь	Ρ	Ъ	Ь	Ъ			P^{2018}	9	Ъ	1
Apogon lachneri *	C,R	Ρ								1		
Apogon maculatus *	C,R	Ъ	Р	Ъ	Р	Ъ		Ъ	P^{2018}	7		
Apogon planifrons *	C,R		Ρ							1		
Apogon townsendi	C,R							Ъ		1		
Astrapogon puncticulatus	C,R										Ъ	
Astrapogon stellatus *	C,R			Ъ		Р				2		
Phaeoptyx conklini *	C,R	Ъ	Ρ	Ъ					P^{2018}	4		
Phaeoptyx pigmentaria *	C,R	Р	Р	Р		Р			P^{2018}	5		
Phaeoptyx xenus * MALACANTHIDAE	C,R	Р	Ъ							2		
Malacanthus plumieri * p	SB	Ŋ	R		Ŋ			LC	R	5		
CORYPHAENIDAE												
Coryphaena hippurus	Р											Р
RACHYCENTRIDAE												
Rachycentron canadum p ECHENEIDAE	Ъ								Ŋ	1		
Echeneis naucrates	Р							R		1		Р
CARANGIDAE												
Caranx bartholomaei p	BP	Ŋ							Ŋ	2		
Caranx crysos * p	BP					0	U		C	3		Р
Caranx hippos p	BP							C ⁶⁶		1		
Caranx latus p	BP	R	0		0			U G**	U	Ś		Р
Caranx lugubris p	BP	Ŋ						0 G**	Ŋ	3		
Caranx ruber p	BP	0	C	0	C	UC		LA G^{88}	LC	7		
Chloroscombrus chrysurus	BP											Ρ
Decapterus macarellus p	Ρ								LC	1		
Decapterus punctatus	Ρ											Ь
Elagatis bipinnulata	Р								R^{2018}	1		
Selar crumenophthalmus	Р											Р
Selene setapinnis	BP											Ρ
Selene vomer	BP								R^{2018}	1		Р
Seriola rivoliana	BP					0			${ m R}^{2018}$	2		Р

Taxon Name	Species Habitat	Triángulo Oeste	Triángulo Este	Obispo Norte	Obispo Sur	Banco Nuevo	Banco Pera	Arenas	Arcas 2016–18	No. reefs	Arenas quadrat	Arcas
Trachinotus carolinus D	BP								R	-	-	
Trachurus lathami	d											d
LUTJANIDAE												
Lutjanus analis p	R						R	G ^{ss}	0	3		
Lutjanus apodus	R		Ŋ					C	U^{2018}	3		
Lutjanus buccanella	R				R			D	0	3		Р
Lutjanus campechanus p	R										Ъ	Р
Lutjanus cyanopterus	R							R	R^{2018}	2		
Lutjanus griseus * p	R	C	C	0	Ŋ	C	D	C G*	C	8		
Lutjanus jocu * p	Я	0	C	Ŋ		Ŋ			C	2		
Lutjanus mahogoni p	R							C	0	2		
Lutjanus synagris p	R							0	0	2		Р
Ocyurus chrysurus * p	BP	U	А	А	C	C	U	${ m A}~{ m G}^{88}$	А	8		
Rhomboplites aurorubens	R,SB											Р
GERREIDAE												
Diapterus rhombeus	SB											Р
Eucinostomus gula p	SB							0	LC	2		Р
Gerres cinereus p	SB							0	Ŋ	2		
HAEMULIDAE												
Anisotremus surinamensis *	R								LC^{2018}	1		
Anisotremus virginicus p	R			R		R		G	LC	4		
Brachygenys chrysargyreum $^{*}\mathrm{p}$	R		0						LC	2		
Emmelichthyops atlanticus p	R	А	LA	C	C	Ŋ			LC	9		
<i>Haemulon aurolineatum</i> * p	R							LC G ⁸⁸	С	2		Ъ
Haemulon carbonarium p	R		N	D	0			R	D	2		
Haemulon flavolineatum * p	R	C	C	C	C	C		$\mathbb{C} \mathbf{G}^{ss}$	C	7		
Haemulon macrostomum p	R	R	0						Ŋ	3		
Haemulon melanurum p	R		0					D	D	3		
<i>Haemulon plumierii</i> *p	R		0	0	0	0	C		Ŋ	9		
Haemulon sciurus p	R							R	Ŋ	2		
Haemulon striatum p	К								LC	1		Р
Haemulon vittatum $^{*}\mathrm{p}$	R	А	LA	C				C	LC	5		

Taxon Name	Species Habitat	Triángulo Oeste	Triángulo Este	Ubispo Norte	Ubispo Sur	Banco Nuevo	Banco Pera	Arenas	Arcas 2016–18	No. reefs	Arenas quadrat	Arcas quadrat
SPARIDAE											q	
Calamus calamus p	SB		R		Я	D	Ŋ	0	C	9		
Calamus nodosus p	SB	R		R				0	C	4		
Lagodon rhomboides	SB											Ρ
Stenotomus caprinus	SB											Ρ
POLYNEMIDAE												
Polydactylus octonemus	SB											Р
Cunoscion diverderius	SR											đ
Commission anthread	as											, C
Cynoscion noinus Fauetus lanceolatus	ac R											- C
Equetus punctatus p	R	Я	R	R				R	Ŋ	5		
Micropogonias undulatus	SB											Р
Odontoscion dentex	R		0							1		
Pareques acuminatus p	R					0	Ŋ	G ^{ss}	Ŋ	4		Р
Pareques umbrosus	R											Ρ
MULLIDAE												
Mulloidichthys martinicus * p	R,SB	C	C	0	C	Ŋ		C G**	C	7		
Mullus auratus	SB											Ъ
Pseudupeneus maculatus * p	R,SB	R	D	0	0	0	0	0 G*	LC	8		
Upeneus parvus DEMDHERIDAF	SB											Ъ
Pempheris schomburgkii * 0	R	Ŋ	Ŋ					LC G ^{ss}	LC	4		
KYPHOSIDAE												
Kyphosus bigibbus p	R	D						R	0	3		
Kyphosus cinerascens p	R	Ŋ						D	C	3		
Kyphosus sectatrix p	R	U	C					$\mathbb{C} \mathbf{G}^{ss}$	C	4		
Kyphosus vaigiensis p CHAETODONTIDAE	R	LC	LC					O	C	4		
Chaetodow catictwatus * 5	Ц	C		11		11		C	C	v		
Chaetodon ocellatus * D	X X		О		С	n n		C G"	0			d
Chaetodon sedentarius * D	R	0	0	0	0	0	Ρ	C G:	U	~ ~~		
Chaetodon striatus * p	R							$\mathbf{U} \mathbf{G}^{ss}$	${ m R}^{2018}$	2		

85

Taxon Name	Species Habitat	Triángulo Oeste	Triángulo Este	Obispo Norte	Obispo Sur	Banco Nuevo	Banco Pera	Arenas	Arcas 2016–18	No. reefs	Arenas quadrat	Arcas quadrat
Prognathodes aculeatus p	R							R		1		4
Holocarthus human dance	D	11	C			C	C	11 088	11	9		
110uuunnnus vermuuensis p Uoloomethaa silismie * 5	4 0	C		11	11	0	4			o v		
	4 6		C	C	C) (- c		
Holacanthus tricolor * p	Х							^ی ۲	Х	7		
Pomacanthus arcuatus $^*\mathrm{p}$	R	D	U	D	D	R	Ъ	0 G**	ГC	8		
Pomacanthus paru * p CIRRHITIDAE	R	0	U			Я	Р	0 G ^{**}	LC	9		Ъ
Amblycirrhitus pinos p POMACENTRIDAE	R,C							Ъ	R	2		
Abudefduf saxatilis * p	R	U	А	U	U			$A G^{88}$	Α	9		
Abudefduf taurus	R								P^{2018}	1		
Chromis cyanea * p	Я	U	U	0	0			LC G ^{ss}	LC	9		
Chromis enchrysura *	R								${ m R}^{2018}$	1		
Chromis insolata p	R							${ m R}~{ m G}^{ m ss}$	LC	2		
Chromis multilineata *	R	А	А	А	А	LC	LC	${ m A}~{ m G}^{88}$	А	8		
<i>Chromis scotti</i> * p	R	C	А	C	C	C	U	LC	C	8		
Microspathodon chrysurus * p	R	U	C	0	0			C G"	U	9		
Neopomacentrus cyanomos * p	R	C	А	0	С	А	C	LC	А	8		
Stegastes adustus * p	R	А	C	C	C			$A G^{88}$	А	9		
Stegastes diencaeus *p	R	D						D	R	4		
Stegastes leucostictus * p	R	LC	LC	Ŋ				LC G ⁸⁸	LC	2		
Stegastes partitus * p	R	Α	А	Α	А	D		$A G^{88}$	А	7		
Stegastes planifrons * p	R	U	C	C	C	C		$O G^{ss}$	А	7		
Stegastes xanthurus * p	R	Υ	U	C	U	C	C	C G ^{ss}	Υ	8		
LADKUDAE Lahrinae												
Bodianus pulchellus p	R		R						LC	2		Ъ
Bodianus rufus * p	R	0	0	0	0	Ŋ		$\mathbb{C} \mathbf{G}^{ss}$	C	7		
Clepticus parrae * p	R	А	А	А	U	U		${ m A}~{ m G}^{88}$	LC	7		
Halichoeres bivittatus p	R	C	C	C	C	C	C	${ m A}~{ m G}^{88}$	Α	8		
Halichoeres burekae * p	R	A	A	Α	A	А	А	Α	A	8		
Halichoeres garnoti * p	R	U	U	C	C	C	U	C G**	C	8		

Taxon Name	Species Habitat	Triángulo Oeste	Triángulo Este	Obispo Norte	Obispo Sur	Banco Nuevo	Banco Pera	Arenas	Arcas 2016–18	No. reefs	Arenas quadrat	Arcas quadrat
Halichoeres maculipinna *	R	С	C	C	C	C	C	$A G^{88}$	С	8	¢	4
Halichoeres pictus	Я											Ρ
Halichoeres poeyi p	R								R	1		
Halichoeres radiatus * p	Я	0	0	0	0	0		G ^{ss}	C	7		
Lachnolaimus maximus * p	R,SB		Я		N	Ŋ	R	G ^{ss}	D	9		
Thalassoma bifasciatum * p	R	C	C	C	U	C	U	${ m A}~{ m G}^{88}$	Α	8	Р	
Xyrichtys martinicensis	SB,R					Ŋ		N		2		
Xyrichtys novacula	SB							N	U^{2018}	2		
Xyrichtys splendens * p	SB					0		Ŋ	D	3		
Scarinae												
Cryptotomus roseus * p	R	R		0	0	0	Ŋ	Ŋ	0	7		
Nicholsina usta	R											Р
Scarus coelestinus p	R		Ŋ					$\mathbf{U} \mathbf{G}^{ss}$	0	3		
Scarus coeruleus * p	R		R				0	$\mathbf{U} \mathbf{G}^{ss}$	С	4		
Scarus guacamaia p	R								0	1		
Scarus iseri * p	R	U	U	C	C	U	U	$\mathbb{C} \mathbf{G}^{\mathbf{ss}}$	U	8		
Scarus taeniopterus * p	Я	D						C G ^{ss}	U	3		
Scarus vetula * p	R	U	U	C	U	0		${ m A}~{ m G}^{88}$	U	7		
Sparisoma atomarium * p	R	R	Ŋ	0	0	0		D	LC	7		
Sparisoma aurofrenatum * p	R	U	C	C	C	U	U	LC G ⁸⁸	U	8		
Sparisoma chrysopterum p	R	R	0		D	0	0	${ m A}~{ m G}^{88}$	0	7		
Sparisoma radians * p	R		0	0	0	D	0	D	U	7		
Sparisoma rubripinne p	R	0	0	Я	D			LC G ⁸⁸	LC	9		
Sparisoma viride * p	R	C	C	C	C	0		U	C	7		
URANOSCOPIDAE												
Astroscopus y-graecum TRIPTERYGIIDAE	SB,C		Ъ							1		
Enneanectes altivelis *	R,SC		Р	Р	Р		Ρ		P^{2018}	5		
Enneanectes boehlkei $^{*}\mathrm{p}$	R,SC			Ρ				Ρ	Р	3		
Enneanectes jordani *	R,SC	C ⁶⁶	Ρ	Р					P^{2018}	4		
DACTYLOSCOPIDAE												
Gillellus greyae *	SB,C								P^{2018}	1		
Gillellus uranidea *	SB,C			Р					P^{2018}	2		

Taxon Name	Species Hahitat	Triángulo Oeste	Triángulo ^{Fste}	Obispo Norte	Obispo	Banco	Banco Pera	Arenas	Arcas 2016–18	No. reefs	Arenas	Arcas
BLENNIIDAE											F	
Entomacrodus nigricans * p	R,SC	Р						C ⁶⁶	D	3		
Hypleurochilus bermudensis *	R,SC	Ρ	Р	Р						3		
Hypsoblennius invemar *p	R,SC								LC	1		
<i>Ophioblennius macclurei</i> * p	R,SC	0		0	0			LC G ^{ss}	C	5		
Parablennius marmoreus * p	R,SC							Ъ	LC	2		
Scartella cristata * p	R,SC	C ⁶⁶							LC	2		
LABRISOMIDAE												
Gobioclinus bucciferus p	R,C	Cé								1		
Gobioclinus gobio *	R,C	Ρ		Ъ					P^{2018}	3		
Gobioclinus guppyi * p	R,C	Ρ	Ρ		Р	Р		C ⁶⁶	P^{2018}	9		
Gobioclinus haitiensis *	R,C		Ρ		Ъ				P^{2018}	3		
Gobioclinus kalisherae * p	R,C	Ρ	Ρ	Р	Ρ			C ⁶⁶	P^{2018}	9		
Labrisomus nuchipinnis ⁻	R,C	Cé							P^{2018}	2		
Malacoctenus aurolineatus * p	R,SC	C ⁶⁶						LC	LC	3		
Malacoctenus macropus * p	R,SC	0	D				0	C	C	5		
Malacoctenus triangulatus [*] p	R,SC	0	0	0	0	0	0	C	C	8		
Paraclinus fasciatus *	R,C								P^{2018}	1		
Paraclinus marmoratus *	R,C					Р	Р			2		
Paraclinus nigripinnis *	R,C				Ρ					1		
Starksia ocellata * p	R,C	Р	Ъ	Р	Р			Р	Р	9		
CHAENOPSIDAE												
Acanthemblemaria aspera *	R,SC	Ρ	Ρ	Р	Р	Р	Ρ	Ъ	P^{2018}	8		
Emblemaria pandionis *	SB,C	Ρ			Р				P^{2018}	3		
Emblemariopsis diaphana *	R,C		Ρ		Р		Ъ	Ъ	P^{2018}	5		
Stathmonotus hemphillii *	R,C								P^{2018}	1		
GOBIESOCIDAE												
Gobiesox strumosus	R,C											Ъ
GOBIIDAE												
Barbulifer ceuthoecus *	R,C								P^{2018}	1		
Bathygobius antilliensis * p, 1	R,SC	C%							P^{2018}	1		
Coryphopterus alloides *	R,C		Р							1		
Coryphopterus dicrus * p	R,SB,SC	0	0	0	0	0	Р	LC	А	8		

Taxon Name	Species Habitat	Triángulo Oeste	Triángulo Este	Obispo Norte	Obispo Sur	Banco Nuevo	Banco Pera	Arenas	Arcas 2016–18	No. reefs	Arenas quadrat	Arcas quadrat
Coryphopterus eidolon *	R,SC	Ρ	Ь	Ρ		Ь		n	P^{2018}	6	I	1
Coryphopterus glaucofraenum p	SB,SC	Р	Ъ				Р	U	А	5		
Coryphopterus hyalinus * p	R	А	А	Р	Р	Р	Р	А	Α	8		
Coryphopterus lipernes *	R,SC			Р						1		
Coryphopterus personatus * p	R	А	А	Р	Р	Р	Р	А	Α	8		
Coryphopterus tortugae *	R,SC	Р		Р					P^{2018}	3		
Ctenogobius saepepallens *	SB,SC								P^{2018}	1		
Ctenogobius stigmaturus p	SB,SC	C ⁶⁶								1		
Elacatinus oceanops *	R,SC	U	C	0	C	0	0	0	C	8		
Elacatinus xanthiprora p	R,C								UC	1		
Gnatholepis thompsoni * p	SB,SC	C	C	C	C	0	0	Α	Α	8		
Gobiosoma grosvenori	R,C											Р
Gobulus myersi *	R,C								P^{2018}	1		
Lythrypnus minimus *	R,C			Ρ					P^{2018}	2		
Lythrypnus nesiotes *	R,C	Ъ	Р	Р	Р					4		
Lythrypnus spilus *	R,C								P^{2018}	1		
Priolepis hipoliti *	R,C			Ρ					P^{2018}	2		
Ptereleotris calliura p	SB		D		D			D	LC	4		
Ptereleotris helenae *	SB		Ъ							1		
Risor ruber *	R,C			Р						1	Р	
ACANTHURIDAE												
Acanthurus chirurgus p	R	0	Ŋ	0	0			$\mathbb{C} \mathbf{G}^{ss}$	C	9		
Acanthurus coeruleus * p	R	C	C	Ŋ	0			${ m A}~{ m G}^{88}$	C	9		
Acanthurus tractus *p	R	C	0	Ŋ	0	Ŋ		${ m A}~{ m G}^{88}$	С	7		
SPHYRAENIDAE												
Sphyraena barracuda * p	Р	C	0	0	Ŋ	Ŋ	R	${ m A}~{ m G}^{88}$	0	8		
Sphyraena borealis	Р			А					LC^{2018}	2		Ъ
Sphyraena guachancho	Ъ											Р
SCOMBRIDAE												
Scomber japonicus	Ъ											Р
Scomberomorus cavalla	Р											Р
PARALICHTHYIDAE												
Citharichthys macrops	SB,C											Ъ

Taxon Name	Species	Triángulo	Triángulo	Obispo	Obispo	Banco	Banco	Arenas	Arcas	No. reefs	Arenas	Arcas
	IIaDItat	Ocste	TSIC	INUTIC	JUL	INUEVO	rera		01-0107		quadrat	quadrat
Cyclopsetta chittendeni	SB,C											Ъ
Cyclopsetta fimbriata	SB,C											Р
Etropus crossotus	SB,C											Ρ
Syacium gunteri	SB,C											Ρ
Syacium papillosum	SB,C											Р
BOTHIDAE												
Bothus lunatus *	R,SB								${ m R}^{2018}$	1		
Bothus ocellatus *	SB,C								P^{2018}	1		
Bothus robinsi	SB,C											Р
ACHIRIDAE												
Gymnachirus nudus	SB,C											Р
Gymnachirus texae	SB,C											Р
CYNOGLOSSIDAE												
Symphurus civitatium	SB,C											Ρ
Symphurus diomedeanus	SB,C											Р
Symphurus minor	SB,C										Ъ	
Symphurus oculellus	SB,C											Р
Symphurus plagiusa	SB,C											Р
Symphurus urospilus BALICTIDAE	SB,C											Р
Ralietae catanicate	D								D	-		đ
Daustes capriscus p	2 4							000 1 1	2 0	- 0		4
Balistes vetula p	R							0 C **	К	2		
Canthidermis sufflamen $^*\mathrm{p}$	R	C	0	Ŋ	Ŋ		R	U G**	0	7		
Melichthys niger p	R	C	0	0	Ŋ	D		LC G ^{ss}	LC	7		
Xanthichthys ringens p MONACANTHIDAE	R							e.	R	2		
Aluterus heudelotii	R											Р
Aluterus scriptus p	R	R		Я				$LC G^{ss}$	0	4		
Cantherbines macrocerus p	R		R		Ŋ			D		3		
Cantherhines pullus * p	R			0				0 G*	R	3		
Monacanthus ciliatus	R										Р	Р
Monacanthus tuckeri *	R				0	Р			LC	\mathcal{C}	Р	
Stephanolepis hispidus	R											Ъ

Taxon Name	Species Habitat	Triángulo Oeste	Triángulo Este	Obispo Norte	Obispo Sur	Banco Nuevo	Banco Pera	Arenas	Arcas 2016–18	No. reefs	Arenas quadrat	Arcas quadrat
OSTRACIIDAE												
Acanthostracion polygonius p	R							Я		1		
Acanthostracion quadricornis	R											Ъ
Lactophrys bicaudalis *	R								R	1		
Lactophrys triqueter * p	R	0	0	0	0	R	R	$O G^{ss}$	0	8		Ρ
TETRAODONTIDAE												
Canthigaster jamestyleri	R		Ъ							1		
Canthigaster rostrata * p	R	C	C	C	C	0	0	C G**	C	8		
Lagocephalus laevigatus	SB											Ъ
Sphoeroides dorsalis	R											Р
Sphoeroides pachygaster	R											Ъ
Sphoeroides spengleri *	R								R^{2018}	1		Р
Sphoeroides testudineus p	R								R	1		
DIODONTIDAE												
Diodon holocanthus	R	R						Я		2		
Diodon hystrix p	R	R	R					0 G*	Ŋ	4		
No. species per reef or		132	131	112	95	80	54	167	209	T=269	13 (7)	127 (93)
Notes relating to taxon nam	es: * Asteris	sk after spec	ies name ind	dicates spec	imen and/o	or tissue spe	scimen was	cataloged i	in UMSND	H collection	n. p after sp	oecies name
indicates existence of publish	ed records (illancis is th	of this speci	ies on the str arm (1 Torn)	udy reefs, a	ll other spe	cies are nev	v records. 1	. Chávez re	ecorded <i>B. s</i>	<i>oporator</i> , fro nly that sne	im which <i>E</i>	8. antillensis 34. R – de-
mersal on reef, SB = demersal	on soft bot	tom, $P = p\epsilon$	ilagic, BP = l	benthopela	gic, C = cry	rptic, SC =	semicryptic	: (more visi	ble than cry	ptic species)). Ranked	au iv = uc- abundance
on reefs (see methods for det	ails): A = a	bundant; C) = common	, widesprea	id; LC = lo	cally comn	non; O = 00	ccasional; l	J = uncomr	non; R = ra	re; P = pre	sent but no
data on abundance; $blank = r$	ot recorde	d on a parti	icular reef or	quadrat. I	No. reefs =	no. reefs oi	n which a s	pecies was	recorded; 2	018 superse	cript: speci	es recorded
at Cayo Arcas by us in 2018 t	out not 201	6. No. spec	sies per reef	or quadra	t: T = total	no. species	recorded o	n reefs by 1	ıs, Garduñc	(1988) or (Chávez (19	66); a (b) =
total no. species in quadrat (n	to. species i	n quadrat t	hat were no	t recorded	by us on an	iy reef). C6	6: species co	ollected by	Chávez (19	66) at Cayo	Arenas and	l Triangulo

Oeste, but not recorded by us. G88: species observed by Garduño (1988) at Cayo Arenas.

Species Notes

These notes refer to information relating to species of particular interest, e.g., those possibly misidentified or which can be confused with other similar species, invasive species, and species that are thought to be reliant on mangroves or seagrass beds for nursery habitats.

Halichoeres burekae Weaver & Rocha, 2007 and H. pictus (Poey, 1860). Halichoeres burekae, a western Gulf of Mexico endemic, is perhaps the most abundant labrid on all eight reefs. This species is listed as Endangered (i.e., at a high risk of extinction) by the IUCN Red List (Rocha et al. 2015) due to the small size of its geographic range and the paucity of reef habitat within that area. The abundance of this species on the west Campeche reefs has substantial conservation significance, as it indicates that the set of small offshore reefs scattered along the western side of Campeche Bank may be essential for its continued existence. None of those reefs are as yet designated as Marine Protected Areas. There is a museum record of H. pictus in the Triángulo Quadrat, although we did not observe this species on any of our study reefs. This species is conspicuous and found on shallow fore-reefs, feeding in midwater in small aggregations in the same habitat as *H. burekae*, which also forms aggregations. Older records of this species on inshore reefs of Veracruz state, and (perhaps) Alacranes reef, may also relate to Halichoeres burekae, a recently described (2007) species endemic to that region, as the latter (but not *H. pictus*) is included in checklists from those reefs published after that date (e.g., González-Gándara 2014; González-Gándara et al. 2012, 2013, Aguilar-Perera and Tuz-Sulub 2009). H. burekae is abundant on the west Campeche reefs, and also common at Alacranes reef and the inshore reefs of Veracruz state.

Halichoeres poeyi (Steindachner, 1867). This species typically is found in seagrass beds around the fringes of Caribbean Reefs. A single specimen of *H. poeyi* was collected at Cayo Arcas in 2018. However, it was not observed by DRR during either the 2016 or 2018 expeditions to that reef or any of the other seven reefs considered here. Hence it must be rare on those reefs. It is present on Alacranes reef (González-Gándara and Arias-González 2001), which has seagrass beds, and on the coastal reefs of Veracruz (del Morales-Flores et al. 2013) that also have adjacent seagrass beds.

Xyrichtys splendens (Castelnau, 1855). This species typically is found in seagrass beds adjacent to Caribbean reefs. On the west Campeche reefs we repeatedly observed small groups of adults associated with concentrations of macroalgae attached to small rocks in and around sandy areas on the leeward sides of reefs.

Stegastes diencaeus (Jordan & Rutter, 1897) and **S. adustus** (Troschel in Muller, 1865). *Stegastes diencaeus* was not observed by DRR at Cayo Arcas in either 2016 or 2018, although we collected one individual there in 2018. This species was present, but uncommon in coralline-rock habitats at ~ 10–15m depth at both Cayo Arenas and Triángulo Oeste. As noted by Robertson et al. (2016b), records by Garduño (1988) of *"Eupomacentrus mellis"*, which is the juvenile of *S. diencaeus* (see Robertson and Allen 1981) on Cayo Arcas quite possibly relate to the similarly colored juveniles of *S. leucostictus* and *S. xanthurus*, which are easily confused with each other. Adults of *S. adustus*,

which are similar in form and color to those of *S.diencaeus* and are easily confused with it (see Robertson et al. 2016b), were abundant on reef habitats with well-developed structure between 0.5–20 m on the five emergent reefs that had such habitat (i.e., all except the three Bancos).

Neopomacentrus cyanomos (Bleeker, 1856). This Indo-Pacific damselfish was locally common to abundant on all reefs we visited, and was observed in aggregations of up to ~ 100 individuals (Robertson et al. 2016a).

Pterois volitans (Linnaeus, 1758). This species was uncommon in the shallow depths at which we dived at all the reefs visited between 2016 and 2018. At Cayo Arcas in 2016 the group of eight divers recorded <12 individuals (Robertson et al. 2016b). A similar number was seen by the group of ten divers who worked at 21 different sites there in 2018. During both the 2016 and 2018 visits a single adult was seen at ~ 30m depth on the oil loading platform 1.5 km from the Arcas reef. At Cayo Arenas the group of seven divers recorded a total less than ten individuals at 38 dive sites visited during May 2017. During the Triángulos trip in 2018 23 divers visited 59 dive sites and noted < 25 individuals in total. At Alacranes Reef on the center of Campeche Bank lionfish is uncommon in shallow water (DRR pers. obs. 2016), and is more abundant at depths below 30m (Aguilar-Perera et al. 2016).

Sphyraena barracuda (Edwards in Catesby, 1771). Adults of all sizes and medium to large juveniles were seen on all eight reefs, with large numbers of subadults (an aggregation of ~ 100 fish, each ~ 70 cm TL on one dive) in the lagoon of the lighthouse island of Cayo Arenas. A few small (3–5 cm) juveniles were observed associated with dislodged clumps of macroalgae on the sand bottom of the lagoon on the leeward side of the lighthouse cay at Cayo Arenas.

Ocyurus chrysurus (Bloch, 1791). This was a common species on all reefs, and present in scores around the Cayo Arcas oil loading platform (see Robertson et al. 2016b). Adults and larger juveniles were both common, and small, recently recruited juveniles ~ 5 cm TL were seen in two situations: (i) a few single individuals were noted with dislodged macroalgae on the 3 m deep floor of the lagoon on the leeward side of the lighthouse island at Cayo Arenas; and (ii) dozens of individuals associated with each of several small (1–2 m diameter) patches of coral debris on sand at ~ 30 m depth on the seaward side of that same reef.

Lutjanus apodus (Walbaum, 1792). Although this species was not observed at Cayo Arcas in 2016, several adults were noted in 2018. At Cayo Arenas in 2018 up to 30 adults of various sizes per dive were recorded on several dives. No small juveniles were seen at either site.

Coryphopterus byalinus Böhlke & Robins, 1962 and *C. personatus* (Jordan & Thompson, 1905). These two small, hovering gobies are very similar in appearance, and are sufficiently similar that usually they are combined in faunal surveys. They were abundant in aggregations of up to hundreds of fish hovering within a meter of the bottom in sheltered habitats on the four emergent reefs abundant and present on the Bancos. Both species were collected at Cayo Arcas in 2018, and subsequently identified in the laboratory, and we assume both were present on the other reefs as well.

Scarus guacamaia Cuvier, 1829. This species was seen on Cayo Arcas reef, in both 2016 and 2018, with ~ 20 small to large adults seen at various different sites on both occasions. However, because the surveys of each reef during the Triángulos expedition were relatively brief, and not specifically aimed at assessing this species, we are uncertain whether this species was present on any of the reefs examined during that expedition. No individuals of this species were seen at Cayo Arcas.

Scarus coeruleus (Bloch, 1786). This species was invariably observed over lowenergy sandy bottoms, notably in the semi-enclosed lagoons on the western sides of reefs. It was common at Cayo Arcas, but none of the other reefs.

Discussion

Comprehensiveness of the faunal lists

Small cryptic fishes commonly represent ~ 40% of the reef-associated shorefish faunas in the neotropics and elsewhere (Smith-Vaniz et al. 2006, Robertson and Smith-Vaniz 2008, Brandl et al. 2018). The most effective way to comprehensively enumerate the cryptic component of the fish fauna of a reef is with the use of small amounts of anesthetics such as clove oil or quinaldine (Robertson and Smith-Vaniz 2010), and small ichthyocide stations (Smith-Vaniz et al. 2006, Robertson and Smith-Vaniz 2008). The latter generally are much more effective than anesthetics at dislodging fishes living deep within the matrices of coralline habitats and allow sampling of larger areas of reef in single stations: -5-10 m diameter vs < 1 m diameter for anesthetics (Robertson and Smith-Vaniz 2008, 2010, and see Goatley et al. 2016). However, as in the present case, use of rotenone often is forbidden by permitting authorities and factors such as cost and local availability determine which anesthetic (clove oil, quinaldine, quinaldine sulphate, MS222) is used in any particular study. Use of clove oil produced specimens of 62 cryptic, reef-associated fish species from the eight reefs we sampled, 26% of the 237 demersal (non-pelagic) fishes we recorded. Cryptic species also represented 35 (74 %) of the 47 species added to the fauna of Cayo Arcas in 2018, and brought the representation of such species up to 24% (47) of the demersal fish fauna (199 species) on that reef. We note however, that the anesthetic stations employed were very small, each using ~ 100 ml of 10% clove oil solution delivered by squirt-bottle that affected much less than 0.25 m² of the surface substratum and superficial crevices. This sampling was aimed primarily at obtaining specimens for a study of connectivity among reef fish populations of the southwest Gulf of Mexico and Caribbean Mexico. Due to time limitations the full variety of types of hard-reef microhabitats and soft-sediment microhabitats within and bordering reef areas were not comprehensively sampled. Hence full documentation of the cryptic reef-fish fauna of these reefs has yet to be done. For example, we collected no ophichthid or congrid eels, no antennariids, gobiesocids, or callyonymids, only a single syngnathid, and no cuskeels. Thus 24% cryptic species likely is an underestimate of that component of the Cayo Arcas demersal fish fauna.

For Cayo Arenas, a reef complex of similar size and form to that at Cayo Arcas, 167 species also seems low, especially given that only 14% (24) of the species currently recorded from there are cryptic. For Triángulo Oeste, the reef most heavily sampled during the 2018 cruise of the *Isla Mujeres*, the cryptic representation was 31% (41) of the 132 species, although the total also seems low, even for reef much smaller than the reefs at either Cayo Arcas or Cayo Arenas. Clearly there is more collecting to be done before the reef-fish fauna of this area can be classed as comprehensively sampled.

Common species on the study reefs: 1980s vs. 2010s

Table 2 includes information on the relative commonness of species at Cayo Arcas and Cayo Arenas during either or both of two periods separated by 30+ years. This list includes species defined as numerically dominant (ie common) at one or both reefs in the 1980s by Garduño and Chávez (2000) and others that were common to abundant during our surveys in 2016–18 but not present in the 1980s list. Among the 42 common 1980s species only seven were relatively uncommon in the 2010s: Lutjanus apodus, Haemulon plumieri (Lacepède, 1801) H. sciurus (Shaw, 1803) and Holacanthus tricolor (Bloch, 1795) at both reefs, and Anisotremus virginicus (Linnaeus, 1758), Brachygenys chrysargeum (Günther, 1859), and Haemulon carbonarium Poey, 1860 at one reef. In contrast 17 species that were common in the 2010s were not listed among the 1980s group. All species on both lists, except Halichoeres burekae, are common and widely distributed inhabitants of Greater Caribbean reefs. Some, but not all, of the differences between the two lists can be attributed to the use of different methodologies: small transects used in the 1980s (see Garduño and Chávez 2000) are less likely to detect locally abundant and patchily distributed species than are the wide-ranging "seascape" visual surveys by us in the 2010s that sampled much larger areas. Exceptions include all seven species common in the 1980s but not the 2010s. Fishing is an obvious factor to consider with most of those seven, particularly species like L. apodus. While we often saw small fishing boats around the reefs during our expeditions they fished during the day several kilometers or more away from the reefs and only came in to shelter at the leeward edges of reefs at night. We saw no fish traps during any of our diving surveys, and the fishing boats were relying on hook-and-line fishing. In addition, the Cayo Arcas reef-system derives a measure of protection from fishing by being in a security exclusion zone, due to its close proximity to major offshore oil installations. However, L. apodus is a nocturnally active species that uses shallow reef habitats as resting sites during the day and migrates distances of up to at least several km away from those reefs to feed at night (Nagelkerken 2009, Hitt et al. 2011, Friedlander et al. 2013). Such diurnal migrations could make it susceptible to off-reef fishing, which could affect populations sheltering on small reefs (cf. Halpern 2004). Differences in methodology could account for some of the species that were common in the 2010s not being so in the 1980s. However, there are some obvious exceptions to that possibility: Stegastes adustus, H. burekae, Scarus iseri (Bloch, 1789) and Sparisoma aurofrenatum (Valenci**Table 2.** Relative abundance of fishes classified as dominant species on Cayo Arcas and Cayo Arenas during 1984–86 by Garduño (1988) as reported in Chávez and Beaver (2007) and our own observations on the same reefs in 2016–18.

Species Areas 2017 Areas 1900 Areas 2010-15 Areas 1900 HOLOCENTRIDAE C YES O YES Erenander and the second of the second o	S	A	A	A	A 1090-
HOLDEENTRUDE HOLDEENTRUDE Holocentra rufus* C YES O YES SERANIDAE Cephalopholis furrifer LC C Epinephelus adacensionis O C Epinephelus adacensionis O YES C YES Gramma lorents* C YES C YES GRAMMATIDAE C TYES C YES CARANGIDAE Caranax ruber LA YES C YES CARANGIDAE Lutjanus apodas O YES U YES Lutjanus apodas O YES U YES Lutjanus apodas O YES A YES Lutjanus analogoni C O Coyura chrystora * A YES A YES HAEMULIDAE HAEMULIDAE Haemuloa nuineatum * C YES U YES Haemuloa fuedomineatum * C YES U YES Haemuloa vitatum * C YES U YES Haemuloa vitatum * C YES U YES Haemuloa vitatum * C YES U YES POMACENTRIDAE FOMACENTRIDAE FOMACENTRIDAE FOMACENTRIDAE FOMACENTRIDAE FOMACENTRIDAE FOMACENTRIDAE FOMACENTRIDAE C YES C YES C YES C YES C YES C YES C YES C YES C YES C YES C YES C YES C Y	Species	Arenas 201/	Arenas 1980s	Arcas 2016–18	Arcas 1980s
Tradectrist rights************************************	HOLOCENIRIDAE	C	VEC	0	VEC
SERRANIDAE SERRANIDAE Gephalapholis is curentata C C cphalapholis is farcifer LC C Epinephelis adaceminis O YES C YES Epinephelis guaratista * O YES C YES GRAMMATIDAE Gramma loreta * C YES C YES GRAMMATIDAE Caratur tuber LC YES C YES LC YES LTJANIDAE Latjanus apodas O YES U YES LC YES LUTJANIDAE Latianus apodas O YES LC YES LC YES LUTJANIDAE Latianus apodas O YES LC YES LLTIJANIDAE LATENULAA A YES LC YES LLTIJANIDAE LATIANIS LC YES LLTIJANIDAE Latianus A YES U YES LATIANISA LC YES LATIANISA LATIANISA LC YES LC YES LATIANISA LATIANISA LC YES LC YES LATIANISA LATIANISA LC YES LC YES LC YES LATIANISA LC YES LC YES LC YES LATIANISA LC YES LC YES LATIANISA LC YES LC YES LC YES LATIANISA LT YES LC YES LC YES LC YES LATIANISA LT YES LT YES LT LT YES LT	Holocentrus rufus *	C	YES	0	YES
Cephalopholis fruentiation C C C C Epinephelus adacensionis O YES C YES Epinephelus adacensionis O YES C YES Epinephelus adacensionis O YES C YES GRAMMATIDAE Granma loreto* LC YES C YES CARANCEDAE CARANCEAE CARANCEDAE CARANCEAE CAR	SERRANIDAE	0		0	
Capital politic functionI.C.C.Epinephole discensionisOCEpinephole discensionisOYESCSerratus tigrinus *CYESCGramma loreto *L.CYESCGramma loreto *L.CYESCCaranex ruberLAYESLCVESUYESLatjanus griesa *CCCOYESUVESLutinus quiesa *AYESAYESLatjanus griesa *COOcytars chrysteris *AYESAnisotremus viginicus-YESLCYESLCHAEMULIDAEAnisotremus viginicus-YESHaemulon aurolineatum *LCYESHaemulon aurolineatum *CYESHaemulon aurolineatum *CYESHaemulon sitrusRYESHaemulon vitatum *CYESHaemulon vitatum *CYESHaemulon vitatum *CYESHaemulon vitatum *CCYESVESCPEMPHERIDAEPempheris schomburgkit *LCYESRYESPempheris schomburgkit *CCChaetodon seellatusCCCYESLCPEMPHERIDAEPomacanthus paru *OYESPomacanthus paru *OYESPomacanthus paru *C<	Cephalopholis cruentata	C		C	
Epinephelus addecessionisOYESCYESSerranus tigrinus *OYESCYESGRAMMATIDAE	Cephalopholis furcifer	LC		C	
Lipinepletus guitatus**OYESCYESCYESCYESGRAMMATIDAE	Epinephelus adscensionis	0	100	С	100
Serranus igrinus * C YES C YES (YES) GRAMMATIDAE Gramma loreta * LC YES C YES CARANGIDAE Garanxa ruber LA YES LC YES CARANGIDAE Garanxa griseus * LC YES Lutjanus apadus O YES U YES Lutjanus apadus C O Ocyurus chrysurus * A YES A YES HAEMULIDAE HAEMULIDAE HAEMULIDAE Haemulon aurolineatum * LC YES LC YES Haemulon carbineatum * LC YES C YES Haemulon fatolineatum * LC YES C YES Haemulon fatolineatum * LC YES C YES Haemulon fatolineatum * C YES LC YES Haemulon fatolineatum * C YES U YES Haemulon scirutus R YES U YES Haemulon fatolineatum * C YES LC YES Haemulon fatolineatum * C YES LC YES Haemulon fatolineatum * C YES LC YES Haemulon binatem * C YES LC YES Haemulon fatolineatum * C YES LC YES Haemulon fatolineatum * C YES LC YES Haemulon scirutus R YES U YES Haemulon scirutus C YES LC YES MULIDAE Mullichthys martinicus * C YES LC YES MULIDAE Fyphosus sectaritis C C C C CHAETODONTIDAE Fyphosus sectaritis C C C POMACANTHIDAE Halenulon site and C YES LC YES PomAcenthus paru * O YES LC YES POMACENTHIDAE Halenulon site and C C C C C CHAETODONTIDAE Halenulon site C C C POMACANTHIDAE Halenulon site and YES A YES PomAcentricae C YES LC YES PomAcentricae C YES LC YES POMACENTRIDAE Halenulon site and A Segastes parting * A YES A YES Chromis souti C C C C Segastes parting * A YES A YES Segastes parting * A YES A YES Segastes parting * A YES A YES	Epinephelus guttatus *	0	YES	С	YES
GRAMMAINIDAE Gramma larven's LC YES C YES CARANGIDAE Caranse ruber LA YES LC YES LUTJANIDAE Lutjanus godus O YES U YES Lutjanus mahogoni C O Cyurus chrysarysen's A YES A YES HAEMULIDAE Anitotrenus virginicus - YES LC YES HAEMULIDAE Anitotrenus virginicus - YES LC YES Bachgenge, Chrysargreum' - YES LC YES Haemulon auvolineatum R YES U YES Haemulon favolineatum C YES C YES Haemulon favolineatum C YES U YES Haemulon sciurus R YES U YES Haemulon sciurus R YES U YES Haemulon vititum C YES LC YES Haemulon sciurus C YES Haemulon sciurus C YES Haemulon carbonaritum C YES U YES Haemulon sciurus C YES C YES Haemulon Sciurus C YES C YES	Serranus tigrinus *	С	YES	С	YES
Gramma laveto* LC YES C YES CARANGIDAE Caranar ruber LA YES LC YES LUTJANIDAE Lutjanus apodus O YES U YES Lutjanus mabogoni C O Cyurus chryaurys* A YES A YES AA YES A YES HAEMULIDAE Anisotremus virginicus - YES LC YES Haemulon dirolineatum * LC YES C YES Haemulon aurolineatum R YES U YES Haemulon flavolineatum * C YES C YES Haemulon flavolineatum * C YES U YES Haemulon sciturus R YES U YES Haemulon sciturus R YES U YES Haemulon vitatum * C YES LC YES Haemulon vitatum * C YES LC YES Haemulon sciturus R YES U YES Haemulon sciturus R YES U YES Haemulon sciturus R YES U YES Haemulon vitatum * C YES LC YES Haemulon vitatum * C YES LC YES Haemulon sciturus R YES U YES Haemulon sciturus R YES LC YES Haemulon sciturus * C C YES Haemulon yitatum * C YES LC YES Haemulon yitatum * C YES LC YES MULliDAE Holacanthus ricitor * R YES R YES POMACANTHIDAE Holacanthus spart * O YES LC YES Chromis soptar * A YES A YES Chromis soptar * C YES LC YES Chromis soptar * A YES A YES Chromis sotii C C C Segastes partitus * A YES A YES Segastes partitus * A YES A YES	GRAMMATIDAE			_	
CARNGIDAE Caranx ruber La YES LC YES LUTJANIDAE Lutjanus apodus O YES U YES U U YES Lutjanus apodus O YES U YES Lutjanus apodus C C C C C C C C C C C C C C C C C C C	Gramma loreto *	LC	YES	С	YES
Caranx ruber LA YES LC YES LUTJANIDAE LUTJANIDAE Lutjanus godus O YES U YES Lutjanus griseus * C G C Lutjanus griseus * C G YES HAEMULIDAE Anisotremus virginicus - YES LC YES HAEMULIDAE Anisotremus virginicus - YES LC YES Brachygenys chrysargyneum * - YES U YES Haemulon carbonarium R YES U YES Haemulon carbonarium R YES U YES Haemulon flavolineatum * C YES U YES Haemulon flavolineatum * C YES U YES Haemulon plumierii * - YES U YES Haemulon plumierii * - YES U YES Haemulon sciurus R YES U YES Haemulon sciurus C YES LC YES Haemulon sciurus C YES LC YES Haemulon sciurus C YES LC YES Haemulon britatum * C YES LC YES Haemulon plumierii * C YES LC YES Haemulon sciurus R YES U YES Haemulon sciurus C C YES LC YES Haemulon sciurus C C YES LC YES Haemulon sciurus C C YES LC YES Haemulon sciurus C YES LC YES POMCHENDAE Kyphosus scatarix C C C YES PAMPHERIDAE Kyphosus vaigiensis C C C Chaetodon scelatus A YES R YES POMCENTINDAE F Pomacanthus priva * O YES LC YES LC YES Chromis scotti C YES C C YES Chromis scotti C C C Segautes partitus * A YES A YES Segautes partitus * A YES A YES	CARANGIDAE				
LUTJANIDAE Lutjanus griesus * Lutjanus griesus * C Lutjanus griesus * C Lutjanus griesus * C C Lutjanus griesus * A YES	Caranx ruber	LA	YES	LC	YES
Lutjanue apodusOYESUYESLutjanue aprisus *CCOOcyurus chrysurus *AYESAYESHAEMULIDAE-YESLCYESHAEMULIDAE-YESLCYESHaemulon aurolineatum *-YESLCYESHaemulon carbonariumRYESUYESHaemulon flavolineatum *CYESUYESHaemulon flavolineatum *CYESUYESHaemulon plunierii *-YESUYESHaemulon plunierii *-YESUYESHaemulon sciurusRYESUYESHaemulon sciurusRYESLCYESMulloidichtys martinicus *CYESLCYESPEMPHERIDAECYESPempheris schomburgkii *LCYESLCYESViphosus sectartixCCCCChaetodon ocellatusCCCYESPOMACANTHIDAEPPomAcentritip sarui*OYESLCYESPOMACENTRIDAEPOMACENTRIDAEChaetodon ocellatusCCCYESChromis cyanea *LCYESAYESChromis cyanea *LCYESAYESChromis cyanea *LCYESAYES </td <td>LUTJANIDAE</td> <td></td> <td></td> <td></td> <td></td>	LUTJANIDAE				
Lutjanus grises *CGLutjanus mahogoniCOOcyurus torpysurus *AYESAYESHAEMULIDAE-YESLCYESBrachygenys chrysargreum *-YESCYESHaemulon aroolineatum *LCYESCYESHaemulon aroolineatum *LCYESUYESHaemulon flavolineatum *CYESUYESHaemulon flavolineatum *CYESUYESHaemulon plunierii *-YESUYESHaemulon plunierii *-YESUYESHaemulon sciurusRYESUYESHaemulon vittatum *CYESLCYESMulloidichthys martinicus *CYESLCYESPEMPHERIDAEYESLCYphosus sectatrixCCCYESChaetodon scellatusCCCYESPOMACANTHIDAEYESPomacanthus part *Holacanthus tricolor *RYESLCYESPOMACANTHIDAEYESPOMACENTRIDAEYESPOMACENTRIDAEYESChromis cyanea *LCYESAYESChromis cyanea *LCYESAYESChromis cyanea *LCYESAYESChromis scottiCC<	Lutjanus apodus	О	YES	U	YES
Lutjanus mahogoni C O O Ocyurus chrysurus ** A YES A YES A YES HAEMULIDAE Anisotremus virginicus – YES LC YES Brachygenys chrysargyreum * – YES LC YES Haemulon aurolineatum * LC YES C YES Haemulon favolineatum * LC YES C YES Haemulon favolineatum * C YES C YES Haemulon favolineatum * C YES U YES Haemulon favolineatum * C YES U YES Haemulon sciurus R YES U YES Haemulon vitatum * C YES LC YES Haemulon sciurus R YES U YES Haemulon vitatum * C YES LC YES PEMPHERIDAE Fulloidichtys martinicus * C C C YES PEMPHERIDAE Kyphosus vaigienis C C C Chaetodon scelentarius C C C Chaetodon scelentarius C C C POMACANTHIDAE Holacanthus tricolor * R YES R YES Pomacanthus paru * O YES LC YES Chaetodon scelentarius C YES Chaetodon scelentarius C YES C YES Chaetodon chrysurus * A YES A YES Chromis cyanea * LC YES LC YES Chromis cyanea * LC YES A YES Stegastes adustus A A Stegastes leucositius * C YES A YES Stegastes leucositius * LC YES A YES	Lutjanus griseus *	С		С	
Ocyurus chrysurus *AYESAYESHAENULIDAE-YESVESAnisotremus virginicus-YESUCYESAnisotremus virginicus-YESLCYESHaemulon aurolineatum *LCYESCYESHaemulon favolineatum *CYESUYESHaemulon fuonierii *-YESUYESHaemulon plunierii *-YESUYESHaemulon vitatum *CYESUYESHaemulon vitatum *CYESUYESMulloidichtys martinicus *CCYESPEMPHERIDAEYESPempheris schomburgkii *LCYESLCViphosus vaigiensisCCCChaetodon scellatusCCCChaetodon scellatusCCYESPOMACANTHIDAEYESPomacanthus paru *OYESLCPOMACANTHIDAE-CYESChromis cyanea *LCYESAChromis scottiCCYESChromis scottiCYESAChromis scottiCYESYESChromis scottiCYESYESChromis scottiCYESYESChromis scottiCYESYESChromis scottiCYESYESStegaste alustusAAYESStegaste alustus * </td <td>Lutjanus mahogoni</td> <td>С</td> <td></td> <td>О</td> <td></td>	Lutjanus mahogoni	С		О	
HAEMULIDAEAnisotremus virginicus-YESLCYESBrachygenys chrysargyreum *-YESLCYESHaemulon carbonariumRYESQYESHaemulon carbonariumRYESUYESHaemulon flavolineatum *CYESQYESHaemulon plumierii *-YESUYESHaemulon sciurusRYESUYESHaemulon vittatum *CYESLCYESHaemulon vittatum *CYESLCYESMULLIDAEVESLCYESYESPEMPHERIDAEVESLCYESPempheris schomburgkii *LCYESLCKyphosus sectatrixCCCKyphosus sectatrixCCCChaetodon ocellatusCCCChaetodon ocellatusCCYESPOMACANTHIDAEVESRYESPOMACENTRIDAEVESICYESPomacanthus paru *OYESAChronis scottiCCYESChronis scottiCCYESChronis scottiCYESICStegastes alustusAYESAStegastes planifions *OYESAYESStegastes planifions *OYESAYESHEICYESYESStegastes planifions *OYESAYESYES <td>Ocyurus chrysurus *</td> <td>А</td> <td>YES</td> <td>А</td> <td>YES</td>	Ocyurus chrysurus *	А	YES	А	YES
Anisotremus virginicus-YESLCYESBrachygenys chrysargyreum *-YESLCYESHaemulon aurolineatum *LCYESCYESHaemulon flavolineatum *CYESUYESHaemulon flavolineatum *CYESUYESHaemulon sciurusRYESUYESHaemulon vittatum *CYESUYESHaemulon vittatum *CYESUYESHaemulon vittatum *CYESUYESMulbidichthys martinicus *CYESLCYESPEMPHERIDAEYESYESPempheris schomburgkii *LCYESLCYESPEMPHERIDAEYESPempheris schomburgkii *LCYESLCYESPomacanthus tricolor *CCCCChaetodon scellatusCCYESYESPomacanthus tricolor *RYESAYESPomacanthus paru *OYESLCYESPOMACENTRIDAECYESPomacanthus paru *AYESAYESChromis multilineata *AYESAYESChromis soutiCCYESStegastes laustusAStegastes laustusAYESAYESStegastes planifons *OYESAYES <td>HAEMULIDAE</td> <td></td> <td></td> <td></td> <td></td>	HAEMULIDAE				
Brachygenys chrysargyreum *-YESLCYESHaemulon aurolineatum *LCYESCYESHaemulon favolineatum *CYESCYESHaemulon flumierii *-YESUYESHaemulon plumierii *-YESUYESHaemulon sciurusRYESUYESHaemulon sciurusRYESUYESHaemulon vittatum *CYESLCYESMultidichtys martinicus *CYESLCYESPEMPHERIDAEYESICPempheris schomburgkii *LCYESLCYESKyphosus sectatrixCCCCKyphosus sectatrixCCCCChaetodon ocellatusCCCCPOMACANTHIDAEHolacanthus paru *OYESLCYESPOMACENTRIDAEHoldefulf saxatills *AYESAYESChromis multilineata *AYESAYESChromis sottiCCYESChromis sottiCYESCYES-Stegaste planiffons *AYESAYESStegaste planiffons *OYESAYES	Anisotremus virginicus	_	YES	LC	YES
Haemulon aurolineatum *LCYESCYESHaemulon favolineatum *CYESUYESHaemulon flavolineatum *CYESUYESHaemulon sciurusRYESUYESHaemulon vitatum *CYESLCYESHaemulon vitatum *CYESLCYESMultiDAEYESPEMPHERIDAE </td <td>Brachygenys chrysargyreum *</td> <td>-</td> <td>YES</td> <td>LC</td> <td>YES</td>	Brachygenys chrysargyreum *	-	YES	LC	YES
Haemulon carbonariumRYESUYESHaemulon flavolineatum *CYESCYESHaemulon sciurusRYESUYESHaemulon sciurusRYESUYESHaemulon sciurusRYESUYESHaemulon vitatum *CYESLCYESMultiDAE </td <td>Haemulon aurolineatum *</td> <td>LC</td> <td>YES</td> <td>С</td> <td>YES</td>	Haemulon aurolineatum *	LC	YES	С	YES
Haemulon flavolineatum *CYESCYESHaemulon plumierii *-YESUYESHaemulon sciurusRYESUYESHaemulon vitatum *CYESLCYESMULLIDAEKCYESYESMULLIDAECYESLCYESPEMPHERIDAECYESLCYESPEMPHERIDAECYESLCYESPEMPHERIDAECCYESYESPOMACANTIDAECCCYESChaetodon ocellatusCCYESYESPOMACANTHIDAECCYESYESPOMACANTHIDAETYESYESYESPOMACANTHIDAETYESYESYESPOMACENTRIDAECYESYESYESPOMACENTRIDAETYESYESYESChoronis cyanea *LCYESYESYESChronis squata *AYESAYESChronis multilineata *AYESAYESChronis scottiCYESCYESStegastes plantifrons *AYESAYESStegastes plantifrons *AYESAYES	Haemulon carbonarium	R	YES	U	YES
Haemulon plumierii *-YESUYESHaemulon sciurusRYESUYESHaemulon vittatum *CYESLCYESMULLIDAE </td <td>Haemulon flavolineatum *</td> <td>С</td> <td>YES</td> <td>С</td> <td>YES</td>	Haemulon flavolineatum *	С	YES	С	YES
Haemulor sciurusRYESUYESHaemulon vittatum *CYESI.CYESMulloidichthys martinicus *CCYESMulloidichthys martinicus *CCYESPEMPHERIDAEYESI.CPemphersi schomburgkii *I.CYESI.CYESKyphosus sectatrixCCCKyphosus sectatrixCCKyphosus sectatrixCCCCCChaetodon ocellatusCCCCCChaetodon sedentariusCCCCCPOMACANTHIDAEVESI.CYESHolacanthus tricolor *RYESRYESPOMACENTRIDAEYESYESAbudefduf saxatilis *AYESAYESChromis cyanea *I.CYESI.CYESChromis sottiCCCYESStegastes dustusAAYESAYESStegastes lausitus *AYESAYESStegastes planifrons *OYESAYES	Haemulon plumierii *	-	YES	U	YES
Haemulon vittatum *CYESLCYESMULLIDAEMulloidichthys martinicus *CCYESPEMPHERIDAECYESLCPempheris schomburgkii *LCYESLCKYPHOSIDAEKCCKyphosus sectatrixCCKKophosus sectatrixCCCCHAETODONTIDAECCCChaetodon ocellatusCCCChaetodon sedentariusCCCPOMACANTHIDAEKYESRYESPomacanthus paru *OYESLCYESPOMACENTRIDAEUVESYESYESPomacanthus paru *AYESAYESChromis cyanea *LCYESLCYESChromis scottiCCYESYESChromis scottiCYESCYESStegastes leucostictus *LCYESAYESStegastes planifrons *OYESAYESStegastes planifrons *OYESAYES	Haemulon sciurus	R	YES	U	YES
MULLIDAEMulloidichthys martinicus*CCYESPEMPHERIDAEICYESICPempheris schomburgkii*ICYESICKYPHOSIDAECCKYPHOSIDAEKyphosus sectatrixCCCKyphosus sectatrixCCCChaetodon ocellatusCCCChaetodon ocellatusCCCPOMACANTHIDAECCCPOMACANTHIDAEUUYESHolacanthus tricolor *RYESRPOMACENTRIDAEUUYESPOMACENTRIDAEUYESYESChromis cyanea *ICYESYESChromis scottiCCYESChromis scottiCYESYESStegastes leucostictus *ICYESYESStegastes paritius *AYESAStegastes planifrons *OYESAYESAYESAYES	Haemulon vittatum *	С	YES	LC	YES
Mulloidichthys martinicus*CCYESPEMPHERIDAEICYESICPempheris schomburgkii*ICYESICKYPHOSIDAECCCKyphosus sectatrixCCCKyphosus sectatrixCCCKyphosus sectatrixCCCKyphosus vaigiensisCCCCHAETODONTIDAECCCChaetodon ocellatusCCCChaetodon sedentariusCCCPOMACANTHIDAEHolacanthus tricolor *RYESRYESPOMACENTRIDAEVESICYESPOMACENTRIDAEUUYESYESPomacanthus paru *OYESICYESChromis cyanea *ICCYESAYESChromis scottiCYESAYESChromis scottiCYESAYESStegastes laustusAYESAYESStegastes laustus *AYESAYESStegastes patinits*AYESAYESStegastes planifrons *OYESAYES	MULLIDAE				
PEMPHERIDAEPempheris schomburgkii *LCYESLCKyphosus sectatrixCCCKyphosus sectatrixCCCKyphosus sectatrixCCCKyphosus sectatrixCCCCHAETODONTIDAECCCChaetodon ocellatusCCCChaetodon sedentariusCCCPOMACANTHIDAEHolacanthus tricolor *RYESRYESPOMACENTRIDAEVESLCYESPOMACENTRIDAEUYESAYESChromis cyanea *LCYESLCYESChromis scottiCCCMicrospathodon chrysurus *CYESAYESStegastes leucostictus *LCLCICStegastes planifrons *OYESAYES	Mulloidichthys martinicus *	С		С	YES
Pempheris schomburgkii*LCYESLCKYPHOSIDAEKYPHOSIDAEKyphosus sectatrixCCKyphosus sectatrixCCKyphosus vaigiensisCCCHAETODONTIDAECCChaetodon ocellatusCCChaetodon sedentariusCCPOMACANTHIDAECCHolacanthus tricolor *RYESPomacanthus paru *OYESLCYESLCPOMACENTRIDAEUAbudefduf saxatilis *AYESChromis cyanea *LCYESChromis scottiCCChromis scottiCYESStegastes adustusAAStegastes leucostictus *LCYESStegastes planifrons *OYESAYESAYESAYES	PEMPHERIDAE				
KYPHOSIDAEKyphosus sectatrixCCKyphosus sectatrixCCKyphosus vaigiensisCCCHAETODONTIDAECCChaetodon ocellatusCCChaetodon sedentariusCCPOMACANTHIDAEUVESHolacanthus tricolor *RYESPomacanthus paru *OYESLCYESLCPOMACENTRIDAEUAbudefduf saxatilis *AYESChromis cyanea *LCYESChromis scottiCCChromis scottiCYESStegastes adustusAYESStegastes leucostictus *LCYESStegastes partitus *AYESStegastes planifrons *OYESAYESAYES	Pempheris schomburgkii *	LC	YES	LC	
Kyphosus sectatrixCCKyphosus vaigiensisCCCHAETODONTIDAECCChaetodon ocellatusCCChaetodon sedentariusCCPOMACANTHIDAEUVESHolacanthus tricolor *RYESPomacanthus paru *OYESLCYESLCPOMACENTRIDAEUAbudefduf saxatilis *AYESChromis cyanea *LCYESChromis scottiCCMicrospathodon chrysurus *CYESStegastes adustusAYESStegastes partitus *AYESStegastes planifrons *OYESStegastes planifrons *OYESAYESAYESYESYESStegastes planifrons *OYESAYESAYESYESYESStegastes planifrons *OYESAYES <td>KYPHOSIDAE</td> <td></td> <td></td> <td></td> <td></td>	KYPHOSIDAE				
ArrowCCKyphous vaigiensisCCCHAETODONTIDAECCChaetodon ocellatusCCChaetodon sedentariusCCPOMACANTHIDAEVESHolacanthus tricolor *RYESPomacanthus paru *OYESLCYESLCPOMACENTRIDAEAbudefduf saxatilis *AYESAbudefduf saxatilis *AYESChromis cyanea *LCYESChromis scottiCCMicrospathodon chrysurus *CYESStegastes adustusAYESStegastes partitus *AYESStegastes planifrons *OYESAYESAYESYESYESStegastes planifrons *OYESCorrents *AYESStegastes planifrons *OYESCorrents *AYESChromis *AYESChromis scottiCYESChromis scottiCYESChromis scottiCYESChromis scottiAYESStegastes planifrons *OYESStegastes planifrons *OYESChromis *OYESChromis *AYESChromis *AYESChromis *AYESChromis *AYESChromis *AYESChromis *AYES <td>Kvphosus sectatrix</td> <td>С</td> <td></td> <td>С</td> <td></td>	Kvphosus sectatrix	С		С	
CHAETODONTIDAEChaetodon ocellatusCCChaetodon sedentariusCCPOMACANTHIDAEHolacanthus tricolor *RYESPomacanthus paru *OYESLCYESOYESLCPOMACENTRIDAEAbudefduf saxatilis *AYESAChromis cyanea *LCYESLCChromis scottiCCCMicrospathodon chrysurus *CYESCStegastes adustusAYESAStegastes partitus *AYESAYESOYESAYESStegastes planifrons *OYESAYESYESAYES	Kvphosus vaigiensis	C		C	
Chaetodon ocellatus C C Chaetodon sedentarius C C POMACANTHIDAE Holacanthus tricolor * R YES R YES Pomacanthus paru * O YES LC YES POMACENTRIDAE Abudefduf saxatilis * A YES A YES Chromis cyanea * LC YES LC YES Chromis scotti C YES A YES Chromis scotti C C C Microspathodon chrysurus * C YES C YES Stegastes adustus A A Stegastes leucostictus * LC LC Stegastes partitus * A YES A YES Chromis * O YES A YES	CHAETODONTIDAE				
Chaetodon sedentariusCCChaetodon sedentariusCPOMACANTHIDAEHolacanthus tricolor *RYESPomacanthus paru *OYESI.CPOMACENTRIDAEICYESAbudefduf saxatilis *AYESAPomacentration s cyanea *LCYESI.CChromis cyanea *LCYESAYESChromis scottiCCCMicrospathodon chrysurus *CYESCStegastes adustusAYESAYESStegastes leucostictus *LCLCLCStegastes partitus *AYESAYESStegastes planifrons *OYESAYES	Chaetodon ocellatus	С		С	
POMACANTHIDAEPOMACANTHIDAEHolacanthus tricolor *RYESRYESPomacanthus paru *OYESLCYESPOMACENTRIDAEAbudefduf saxatilis *AYESAYESChromis cyanea *LCYESLCYESChromis scottiCCCMicrospathodon chrysurus *CYESCYESStegastes adustusAYESAYESStegastes partitus *AYESAYESStegastes planifrons *OYESAYES	Chaetodon sedentarius	C		Ċ	
Holacanthus tricolor *RYESRYESPomacanthus paru *OYESLCYESPOMACENTRIDAEAbudefduf saxatilis *AYESAYESChromis cyanea *LCYESLCYESChromis scyanea *LCYESAYESChromis scottiCCCMicrospathodon chrysurus *CYESCYESStegastes adustusAAAStegastes leucosticitus *LCLCStegastes partitus *AYESAYESStegastes planifrons *OYESAYES	POMACANTHIDAE				
Pomacanthus paru *OYESLCYESPOMACENTRIDAEAbudefduf saxatilis *AYESAYESChromis cyanea *LCYESLCYESChromis scottiCYESAYESChromis scottiCCCMicrospathodon chrysurus *CYESCYESStegastes adustusAAAStegastes adustusAStegastes partitus *AYESAYESStegastes planifrons *OYESAYES	Holacanthus tricolor *	R	YES	R	YES
POMACENTRIDAEICICICAbudefduf saxatilis *AYESAYESChromis cyanea *LCYESLCYESChromis multilineata *AYESAYESChromis scottiCCCMicrospathodon chrysurus *CYESCStegastes adustusAAStegastes leucostictus *LCStegastes partitus *AYESAYESStegastes planifrons *OYESAYES	Pomacanthus paru *	0	YES	IC	YES
Abudefduf saxatilis * A YES A YES Abudefduf saxatilis * A YES A YES Chromis cyanea * LC YES LC YES Chromis multilineata * A YES A YES Chromis scotti C C C Microspathodon chrysurus * C YES Chromis scotti C YES C YES YES Stegastes adustus A A A YES Stegastes leucostictus * LC LC Stegastes partitus * A YES A YES YES Stegastes planifrons * O YES A YES	POMACENTRIDAE	Ũ	TEO		110
Initial of the second statementInitial of the second statementInitial of the second statementChromis cyanea *LCYESLCYESChromis multilineata *AYESAYESChromis scottiCCCMicrospathodon chrysurus *CYESCYESStegastes adustusAAAStegastes leucostictus *LCLCLCStegastes partitus *AYESAYESStegastes planifrons *OYESAYES	Abudefduf saxatilis *	А	YES	А	YES
Chromis multilineata *AYESAYESChromis scottiCCCMicrospathodon chrysurus *CYESCYESStegastes adustusAAAStegastes leucostictus *LCLCLCStegastes partitus *AYESAYESStegastes planifrons *OYESAYES	Chromis cvanea *	IC	YES	IC	YES
Chromis matulation A FLS A FLS Chromis scotti C C C Microspathodon chrysurus * C YES C YES Stegastes adustus A A A Stegastes leucostictus * LC LC Stegastes partitus * A YES A Stegastes planifrons * O YES A	Chromis multilineata *	A	VES	A	VES
Microspathodon chrysurus * C YES C YES Stegastes adustus A A A Stegastes leucostictus * LC LC Stegastes partitus * A YES A Stegastes planifrons * O YES A	Chromis scotti	C	11.5	C C	125
Stegastes adustus A A Stegastes leucostictus* LC Stegastes partitus* A YES A Stegastes planifrons* O	Microspathadan chrystory *	C	VES	C	VES
Stegastes latistics A A Stegastes leucostictus * LC LC LC Stegastes partitus * A YES Stegastes planifrons * O YES	Stanaetae aduetue	Δ	1120	Δ	110
Stegastes partitus * A YES A YES Stegastes planifrons * O YES A YES	Stegastes laucostistus *			л I С	
Stegastes planifrons * O YES A YES	Stagastes bartitus *	A	VES	LC ۵	VES
Sugasus punificitis O IES A IES	Sugartes parinus Stegastes planifroms *	л О	VES	Δ.	VES
Steastes vanthurus * C YES A	Stegastes vanthurus *	C	VES	A	11.0

Species	Arenas 2017	Arenas 1980s	Arcas 2016–18	Arcas 1980s
LABRIDAE				
Clepticus parrae *	А	YES	LC	YES
Halichoeres bivittatus	А		А	
Halichoeres burekae	А		А	
Halichoeres garnoti *	С	YES	С	YES
Halichoeres maculipinna *	А	YES	С	YES
Halichoeres radiatus *	-		С	
Thalassoma bifasciatum *	А	YES	А	YES
SCARIDAE				
Scarus coeruleus *	U	YES	С	YES
Scarus iseri	С		С	
Scarus taeniopterus *	С	YES	С	YES
Scarus vetula *	А	YES	С	YES
Sparisoma aurofrenatum *	LC		С	
Sparisoma chrysopterum	А	YES	О	YES
Sparisoma rubripinne	LC		LC	YES
Sparisoma viride *	С	YES	С	YES
ACANTHURIDAE				
Acanthurus chirurgus	С	YES	С	YES
Acanthurus coeruleus *	А	YES	С	YES
Acanthurus tractus *	А	YES	С	YES
SPHYRAENIDAE				
Sphyraena barracuda *	А		О	
BALISTIDAE				
Melichthys niger	LC	YES	LC	
TETRAODONTIDAE				
Canthigaster rostrata *	С	YES	С	YES

Notes: * **Asterisk** after species name indicates specimen and/or tissue specimen was cataloged in UMSNDH collection. **Habitat:** R = demersal on reef, SB = demersal on soft bottom, P = pelagic, BP = benthopelagic, C = cryptic, SC = semicryptic (more visible than cryptic species). **Ranked abundance on reefs (see methods for details):** A = abundant; C = common, widespread; LC = locally common; O = occasional; U = uncommon; R = rare; P = present but no data on abundance; blank = not recorded on a particular reef or quadrat. **No. reefs** = no. reefs on which a species was recorded by us; **2018 superscript:** species recorded by us in 2018 but not 2016. **No. species per quadrat:** a (b) = total no. species in quadrat (no. species in quadrat that were not recorded by us on any reef).

ennes in Cuvier and Valenciennes, 1840) all of which are common throughout a wide range of habitats today and are susceptible to being counted in transects. *Halichoeres burekae* was exceptionally abundant and widely distributed across a range of habitats in the 2010s. Although this species was not described and named until 2007 there are no references made to any species similar to it (e.g., *Halichoeres pictus*) in the 1980s. There is no obvious reason why there was no mention of these four species in the 1980s.

"Mangrove/seagrass nursery species" of reef fishes at isolated Greater Caribbean reefs that lack adjacent nursery habitat(s)

A series of studies have developed around the hypothesis that certain common species of reef fishes in the Greater Caribbean use mangroves and seagrass beds as nurseries (hereafter nursery-species) and are sufficiently reliant on one or both of those as nursery habitats that their local abundances reflect the local availability of those nursery habitats adjacent to reefs (e.g., Nagelkerken et al. 2000, 2017, Serafy et al. 2003, Dorenbosch et al. 2004, 2006, 2007, Halpern 2004, Mumby et al. 2004, Scharer et al. 2007, Scharer 2009, Jones et al. 2010, Claydon et al. 2015). Those studies have relied primarily on examination ofreef areas that contain such habitats, in either variable amounts or at varying distances from local reefs within large reef complexes. However, a few studies have examined nursery-species at locations that lack mangroves but have seagrass beds (Scharer 2009; Aguilar-Perera and Hernández-Landa 2017).

Below we summarize information on the occurrence and, in some cases, abundance of 16 species of reef-fishes commonly regarded as nursery-species in the faunas of various isolated Caribbean reefs that lack mangroves, and, in some instances, seagrass beds. Campeche Bank offshore reefs are among them.

Campeche outer bank reefs. Table 3 contains information on the abundances of nursery-species on West Campeche reefs (no mangroves or seagrasses) and Alacranes reef (seagrasses only). Of those, all are common on Alacranes except *Lutjanus apodus* and *Scarus taeniopterus* (Lesson in Bory de Saint-Vincent, 1829). Eight species are common on West Campeche reefs, including *Scarus taeniopterus*, one (*Haemulon parra* (Desmarest, 1823)) is absent on West Campeche reefs and the remaining six are uncommon. The vast area (~ 100,000 km²) of Campeche bank is relatively shallow, with depths of 30–50 m in most parts. Inter-reef areas comprise a mixture of soft bottoms and small patches of coral and sponges (Hedgpeth 1954, Logan et al. 1969). Bycatch from shrimp trawlers working on soft bottoms on the part of Campeche bank south of the study reefs that were recorded by Hildebrand et al. (1964) included three of the 16 nursery species: *Lutjanus griseus* (Linnaeus, 1758), *Ocyurus chrysurus*, and *Haemulon plumieri*.

Veracruz (Mexico) coastal reefs. Published checklists are available for seven coastal reefs in the northern part of Veracruz state. Of those reefs six are emergent and one submerged, none have mangroves and only two of the emergent reefs have seagrass beds (Table 4). Those reefs vary in their degree of isolation from the mainland coast and from each other. Mexican government chart SM 030 indicates those reefs are all on the continental shelf in water less than ~ 50 m deep, 5–20 km from the coast. The nature of the inter-reef bottoms in that area is unclear. González-Gándara (2014) used an extensive set of surveys to define the fish fauna of Blake Reef, a small (2.5 km long) submerged (minimum depth 9 m) reef that is isolated from both the shore and emergent reefs (20 km from the shore, 36 km from the nearest emergent reef). That reef lacks both seagrasses and mangroves, and the top surface is a plain covered with boulders, corals and sponges (C González-Gándara pers. comm. to DRR 2018). Of the 16 nursery species, only four are not listed at Blake Reef (Table 4). On the six emergent reefs (González-Gándara et al. 2012, 2013) the only nursery species that were absent on all but one reef were *Haemulon parra* and *H. sciurus*.

Flower Garden Banks. These banks are two submerged patches of coral reef located 180 km offshore from the coast of Texas, on the continental shelf. Minimum depth is 17 m, the banks are surrounded by water >50 m deep, and there are no seagrasses or mangroves. Muñoz et al. (2017) found seven nursery species present during quantita-

99

Species	Mangroves	Seagrass	W Campeche	Alacranes
Mangrove & seagrass present?		0	Neither	Seagrass
Lutjanus analis	++	++	Rare	Common
Lutjanus apodus	++	+	Occasional	Uncommon
Lutjanus griseus	++	++	Common	Common
Lutjanus mahogoni	++	++	Locally Common	Common
Ocyurus chrysurus	++	++	Abundant	Abundant
Haemulon flavolineatum	++	++	Common	Common
Haemulon parra	++	+	Absent	Common
Haemulon plumieri	++	++	Occasional	Common
Haemulon sciurus	++	++	Uncommon	Common
Chaetodon capistratus	++	+	Occasional	Common
Scarus coeruleus	+	+	Locally common	Common
Scarus guacamaia	++		Uncommon	Common
Scarus iseri	+	++	Common	Abundant
Scarus taeniopterus	++	+	Common	Uncommon
Acanthurus chirurgus	+	+	Common	Common
Sphyraena barracuda	++	+	Common	Common

Table 3. Sixteen species of common Greater Caribbean reef-fishes thought to be reliant on mangroves and seagrass beds as near-reef nursery habitats, and their general abundance on the west Campeche study reefs and Arrecife Alacranes.

Notes: ++ indicates strong dependency, + weaker dependency. Sources: Usage of seagrass and mangroves as reef fish nurseries: Nagelkerken et al. 2000a, b, 2001, 2017; Cocheret de la Morinière et al. 2002; Nagelkerken and van der Velde 2003; Halpern 2004; Mumby et al. 2004; Dorenbosch et al. 2004, 2006, 2007; Verweij et al. 2008; Nagelkerken 2009; Scharer 2009, Machemer et al. 2012, Harborne et al. 2015, Serafy et al. 2015. Claydon et al. 2015. W Campeche: a summary of results presented here. Fishes of Alacranes reef: González-Gándara and Arias-González 2001, abundance based on observations by DRR during dives at 23 different sites at Alacranes reef during May 2016.

Table 4. Sixteen mangrove/seagrass nursery-fishes present at reefs lacking mangroves, and, in some cases, seagrasses, on the continental shelf near Tuxpan, Veracruz, Mexico.

Species	Lobos	Medio	Blanquilla	Blake	Tanhuijo	Enmedio	Tuxpan
Submerged/Emergent	Emergent	Emergent	Emergent	Submerged	Emergent	Emergent	Emergent
Mangrove/Seagrass	No/Yes	No/No	No/No	No/No	No/No	No/No	No/Yes
Distance from mainland (km)	11.5	7.5	5	20	10	10	13
Fish Species							
Lutjanus analis					Yes	Yes	Yes
Lutjanus apodus	Yes	Yes	Yes	Yes		Yes	Yes
Lutjanus griseus	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Lutjanus mahogoni	Yes		Yes	Yes	Yes	Yes	Yes
Ocyurus chrysurus	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Haemulon flavolineatum	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Haemulon parra			Yes				
Haemulon plumieri	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Haemulon sciurus					Yes		
Chaetodon capistratus	Yes	Yes		Yes	Yes	Yes	Yes
Scarus coeruleus	Yes	Yes			Yes		
Scarus guacamaia	Yes	Yes		Yes		Yes	Yes
Scarus iseri	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Scarus taeniopterus	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Acanthurus chirurgus	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Sphyraena barracuda	Yes		Yes	Yes	Yes	Yes	Yes

Sources: González-Gándara et al. 2013, González-Gándara 2014

tive surveys, four of them moderately common (Table 5). For most of the nursery species not recorded by those authors or by the Flower Garden Bank MPA website, these banks were either out of or at the latitudinal limit of their geographic range, and hence the species would not likely be common enough to be registered by Muñoz et al. (2017)

Navassa Island. This 3.5 km-long island has a narrow fringing reef and rises abruptly out of deep water between Haiti and Jamaica. It is 57 km from land and separated from the shelf around Hispaniola by 35 km of deep (>1000 m) water. Almost the entire reef is 25 m or deeper. Navassa has no mangroves or seagrass beds, but does have substantial stands of macroalgae. The island's limited reef area likely is overfished by subsistence fishers from Haiti (Miller 2002, Sandin 2002). Ten nursery species are present at the island, most of them common (Table 5). Although there are few haemulids and lutjanids at this island, two nursery species dominated the biomass of carnivores at the beginning of the 2000s: *Lutjanus apodus* and *Sphyraena barracuda*.

Mona Island. Mona Island is a 10 km long island that arises precipitously out of deep water, has a narrow shallow fringing reef, no mangroves in the sea and only $\sim 1 \text{ km}^2$ of seagrass, in beds or mixed with rubble, corals, bedrock and sand patches (Scharer 2009). Located in the channel between Hispanola and Puerto Rico, this island is separated by 60–70 km from those two large mangrove bearing islands. Scharer (2009) examined habitat usage and various aspects of the ecology of the reef-fish fauna, focusing in particular on ontogenetic changes in habitat usage by nursery species. Of the 16 nursery species, seven were common, seven were uncommon, and two were absent (Table 5). Abundances of three nursery species are of particular interest: Lutjanus apodus and Lutjanus mahogoni (Cuvier in Cuvier and Valenciennes 1828) were common, and Haemulon parra was moderately common (Scharer 2006). Scharer (2009) and Scharer et al. (2007) found that nursery habitat usage by eight common species for which sufficient data were available for analysis had the following characteristics: nursery habitats typically were shallow; the smallest juveniles were concentrated in seagrass habitats, although most also used hard bottoms; juveniles expanded the range of nursery habitats they used as they grew.

Saba Bank. This large $(2,200 \text{ km}^2)$ submerged coralliferous bank that lacks both seagrass and mangroves is separated by a narrow (several km) stretch of deep water from Saba Island, 6 km away. Minimum depth of the bank is ~ 11 m. There are no mangroves on Saba Island and the only seagrasses there are small patches of *Syringo-dium*. Toller et al. (2010) and Williams et al. (2010) documented the reef-fish fauna of Saba bank, where 11 nursery-species are present, six of them common (Table 5).

Swan Islands. This doublet of islands is situated in deep water 170–180 km offshore from Honduras and the nearest emergent reefs. The area of shallow reef is ~ 8X3 km, and neither island has mangroves. Whether or not there are seagrasses is unclear. The only known survey of the reef-fishes of that island is by AGRRA (http://www. agrra.org/), which uses counts of fishes on small transects, which are likely to miss large, mobile, wide ranging species that avoid divers. That survey, which was made in 2013, and is far from complete, listed 64 species, including 12 of the 16 nursery species (Table 5).

Table 5. Occurrence of 16 mangrove/seagrass nursery-fishes at isolated, emergent, and submerged reefs
n the northern Gulf of Mexico and the Caribbean that lack mangroves, and, in some cases, seagrass
nursery habitats.

Species	Mona Island	Swan Island	Flower Garden Banks	Saba Bank	Navassa Island
On continental shelf?	No	No	Yes	No	No
Isolation distance (Km)	60	170	180	30*	35
Submerged/Emergent	Emergent	Emergent	Submerged	Submerged	Emergent
Mangrove/Seagrass	No/Yes	No/No	No/No	No/No	No/No
Fish Species					
Lutjanus analis	Uncommon		(Out of range)		
Lutjanus apodus	Common	Present	Present (Limit of range)	Present	Common
Lutjanus griseus	Uncommon		Common		
Lutjanus mahogoni	Common	present	Uncommon (Limit of range)	Common	
Ocyurus chrysurus	Uncommon	present	Uncommon	Present	Uncommon
Haemulon flavolineatum	Common	Present	(Out of range)	common	Uncommon
Haemulon parra	Common		(Limit of range)		
Haemulon plumieri	Uncommon	present	Uncommon	Common	
Haemulon sciurus	Uncommon	Present	(Out of range)		Uncommon
Chaetodon capistratus	Common	Present	(Limit of range)	Present	Uncommon
Scarus coeruleus			(Out of range)		Uncommon
Scarus guacamaia	Present	Present	(Out of range)	Present	
Scarus iseri	Common	present	Common (Limit of range)	Common	Uncommon
Scarus taeniopterus	Common	present	Common (Limit of range)	Common	Uncommon
Acanthurus chirurgus	Uncommon	present	Common	Common	Uncommon
Sphyraena barracuda	Uncommon	present	Present	Common	Common

Sources: Mona – Scharer (2009) and see species account; Swan – Aggra (2013); Flower Garden Banks – Muñoz et al. (2017) and https://flowergarden.noaa.gov/about/fishlist.html; Navassa – McClellan & Miller (2002), Collette et al. 2003; Saba – Toller et al. 2010 (abundance data), Williams et al. 2010 (presence/absence)(* Saba Island, 6 km from, and separated by several kilometers of very deep water from Saba Bank, lacks mangroves and *Thalassia*, and the nearest location with *Thalassia* is St. Eustatius island, 30 km from that bank). Out of range: site is outside the geographic range of the species. Limit of range: site is at or near latitudinal limit of the geographic range of the species.

Individual nursery-species accounts (composites from island-fauna accounts)

Lutjanidae. Lutjanus analis (Cuvier in Cuvier and Valenciennes, 1828) uses a variety of habitats as nursery habitat (Lindeman et al. 2016a), in addition to mangrove and seagrasses. It varies from being absent to common on reefs lacking nearby mangroves (Tables 3–5), and generally is rare to absent on reefs without both mangroves and seagrass beds, indicating it may well be dependent on such habitats as nurseries. Juveniles of *L. apodus*, another "mangrove-dependent" nursery species, also use rocky habitat as nursery (Lindeman et al. 2016b). It is sometimes common at sites without mangrove that have seagrasses, which also is used as nursery habitat (Hildebrand et al. 1964), and can be present in significant numbers at sites without either habitat (Tables 3–5). Halpern (2004) suggested that the population at Navassa Island was maintained by immigration from Haiti. However, this is extremely unlikely given the large distances involved; the fact that *Lutjanus apodus* is a demersal species not known to extend below 156 m, and that most of the distance between Hispaniola and Navassa is very deep water. Lutjanus griseus is another nursery species, the juveniles of which also use estuaries (Lindeman et al. 2016c). It is common at isolated reefs on the continental shelf that lack mangroves, and in some cases, seagrasses, but is absent on most isolated oceanic reefs lacking such habitat (Table 3-5). Which habitats are crucial for producing this distribution pattern is far from clear. Lutjanus mahogoni is thought to be weakly dependent on nursery habitats, and can be common at sites without either nursery habitat. Ocyurus chrysurus uses a variety of microhabitats as nurseries, including hard bottom, in addition to mangroves and seagrass beds (Lindeman et al. 2016d, Hildebrand et al. 1964). Large areas of inter-reef substrata scattered over the 100,000+ km² of Campeche Bank that have small patches of rubble microhabitat we saw used by this species as nursery could sustain large populations of this species on the small shallow and emergent reef areas lacking mangroves or seagrasses along the western edge of Campeche Bank. Lutjanids are also known to migrate appreciable distances over shallow shelf habitats, as much as 65 km in the case L. griseus (see Nagelkerken 2009). Such relocation across shallow shelf areas, particularly those with stepping-stone patches of submerged reefal habitat, such as sponges (Hedgepeth 1954, Hildebrand et al. 1964), could account for populations of this species on on-shelf reefs far from nursery habitat, at least 180 km in the case of the Flower Garden Banks. Known diel movements of L. apodus and L. analis to off-reef habitats from daytime resting areas on emergent reefs are much shorter, on the order of < 10 km (Hitt et al. 2011, Friedlander et al. 2013), but a capacity for such activity could be sufficient to provide connectivity across shallow shelves that have scattered patches of submerged reefal habitats (e.g., sponge beds), or increase the susceptibility of fish observed on reefs during the day to fishing some distance away from those reefs.

Haemulidae. Haemulon flavolineatum (Desmarest, 1823) is common on all reefs within its geographic range, regardless of the mangrove/seagrass status of those reefs (Tables 3-5). Haemulon parra, which is classed as seagrass-dependent for nursery habitat (and see Hildebrand 1964), appears to be one of the few species that typically is absent on reefs lacking such habitat (Tables 3-5). Haemulon plumieri has been classed as mainly mangrove dependent (Table 3), but commonly uses shallow hard bottoms and seagrass beds as nurseries (Lindeman et al. 2016e). It is found, often commonly, on reefs without either mangroves or seagrass beds. Haemulon sciurus has been classed as mainly mangrove-dependent, but also using seagrass and hard-bottoms as nursery habitat (Table 3). It is present on reefs lacking mangroves, but uncommon to absent on those without seagrass beds (Tables 3-5). Information available on the mobility of grunts such as H. flavolineatum, H. plumieri, and H. sciurus, indicates that they range over relatively short distances, < 5 km (Friedlander et al. 2013). Whether or not this capacity for mobility is sufficient to allow grunts to move across large distances of shelf between the shore and isolated on shelf reefs is unclear. Perhaps it does for *H. plumieri*, which is trawled in inter-reef areas on Campeche Bank where unnamed, submerged coral and sponge patches are common.

Chaetodontidae. Chaetodon capistratus Linnaeus, 1758 has been classed as mangrove-dependent (Table 3), but is present, sometimes common, on reefs without mangroves, and, in some cases, without seagrasses. This species evidently is capable of maintaining significant local populations using other nursery habitats.

Scaridae. *Scarus coeruleus* has sometimes been classed as mangrove/seagrass nursery dependent (Table 3). Its adults typically feed on low-energy sandy bottoms (Rocha et al. 2012, DRR pers. obs.). It does occur, sometimes commonly, on isolated reefs lacking one or both nursery habitats, and its occurrence may also be influenced by the availability of suitable sandy habitat for adults.

The Rainbow parrotfish, *Scarus guacamaia*, which reaches 120 cm TL, is the largest parrotfish in the Greater Caribbean. It is typically observed in small groups or schools that roam over large areas (Mumby et al. 2004). It is typically seen feeding in shallow reef-edge habitats, including intertidal areas, in water < 5 m deep (Claydon et al. 2015, Hernández and Aguilar-Perera 2018, DRR pers. obs.), although its depth range extends down to at least 55 m (MT Scharer pers. comm. December 2018). This iconic reef-fish is thought to be strongly reliant on mangroves as nursery habitat (Mumby et al. 2004, Claydon et al. 2015, and see studies cited in Table 2), to the extent that removal of mangroves can result in local extinction (Mumby et al. 2004).

Various studies of the habitat distributions of different size classes of S. guacamaia elsewhere have indicated that (i) juveniles observed in mangroves usually are $\sim 10-20$ cm (range 5-60 cm)TL (Dorenbosch et al. 2006; Nagelkerken and Van der Velde 2003, Nagelkerken 2009, Sefay et al. 2003, Jones et al. 2010, Claydon et al. 2015) and that the smaller numbers of juveniles seen in seagrasses near mangroves are somewhat larger than those in mangroves (Nagellkerken et al. 2002, 2009), indicating a shift from mangroves to seagrasses during development. None of those papers provided information on nursery habitats used by juveniles smaller than ~ 5 cm. More recently, however, Aguilar-Perera and Hernández-Landa (2017) observed juveniles 5-10 cm TL in shallow coralrubble habitat on the reef top at Alacranes reef on Campeche bank, as well as adults and substantial schools of large juveniles on that reef. Those authors pointed out that juvenile Scarus guacamaia are not known from the nearest mangroves along the Gulf coast of the Yucatán peninsula, that the nearest coral reefs with adjacent mangroves are 300 km away. They proposed that the Alacranes population of this species is self-sustaining in the absence of mangrove habitat. Although, as noted above, there is one small patch of mangroves associated with a pond at the southeast corner of Isla Perez at Alacranes reef (Tunnell and Chapman 2001), due to its tiny size (~ 0.1 ha) and semi-isolated status that patch is unlikely to act as a significant piece of reef-fish nursery habitat. Long before Aguilar-Perera and Hernandez-Landa's (2017) observations, Hildebrand et al. (1964) collected even smaller juveniles (3-4 cm) of this species in the extensive Thalassia beds at Alacranes reef using push nets, and considered those beds to be nursery habitat for this species. These two studies show that, on mangrove-free reefs, adequate nursery habitats for S. guacamaia can be present in the form of seagrass beds for the smallest juveniles after pelagic larvae recruit there, with shallow rocky habitats acting as secondary nursery habitat for somewhat larger juveniles that typically are seen in mangroves at other locations.

Claydon et al. (2015) examined the distribution of *S. guacamaia* on shoreline reefs at Bonaire, under the assumption that use of mangrove nurseries is obligatory for this

species and the only nursery habitat of importance at that island. They found substantial densities of adults as much as 42 km from the nearest mangroves and assumed they had migrated such distances along the continuous shallow coastline reef. They also found very low densities of this species at a small, mangrove-free island (Klein Bonaire) separated from Bonaire by < 1km of water that has minimum depths of 80 m, and concluded that this was due to lack of immigration from Bonaire.

This species is now known to occur in appreciable numbers at a variety of isolated sites that lack mangroves and, in some cases seagrasses. This includes Cayo Arcas (150 km from the mainland shore), which, like other small, west Campeche emergent reefs, has many reef habitats found on Alacranes reef. If the population of *S. guacamaia* at Alacranes is self-recruiting then the assumption that that is the case with the Cayo Arcas population is reasonable. The small size of individual West Campeche reefs could make it difficult to sustain populations of large, low density species like *S. guacamaia*, and account for the apparent absence of this species on Cayo Arenas. The alternative to juvenile recruitment onto Cayo Arcas would be very long-distance migration, as the nearest reefs with adjacent mangroves are 350 km away in Veracruz state, while Alacranes reef is 330 km from Cayo Arcas, and 170 km from Cayo Arenas.

Scarus guacamaia also occurs on other emergent and submerged reefs lacking mangroves and, in some cases, seagrasses that are situated on the continental shelf but located away from the shoreline in Veracruz state, in the southwest Gulf of Mexico and in Venezuela. In Venezuela this species occurs at three archipelagos of small, rocky islands that lack structural coral reefs and mangroves, and in some cases seagrasses, that are found on the continental shelf off the coast of Venezuela. At each archipelago small groups (~ 6 fish) of adults were seen by DRR at multiple dive sites: Los Monjes at the mouth of the Gulf of Venezuela, 35-40 km from the shore of the Guajira Peninsula Colombia (DRR pers. obs. 2008), Los Frailes, 13 km from mangrove-bearing Isla Margarita (DRR pers. obs. 2005), and Los Testigos, ~ 70 km from both Los Frailes and the shore of the Paria Peninsula (DRR pers. obs. 2006). Depths of the shelf between those islands and the mainland are ~ 30-50 m. While at Isla Margarita in 2005 DRR saw a large adult (~ 1 m TL) of S. guacamaia that had been freshly caught be a shrimp trawler in shallow water ca. 1.5 km offshore from that island. This indicates that adults of this species do sometimes move through inter-reef areas of soft bottoms, although how far from reef habitat that individual was caught is not clear. The known depth range of S. guacamaia extends down to 55 m (MT Scharer, pers. comm. to DRR, December 2018). Hence, while it is feasible for a large species like S. guacamaia to have migrated to those isolated reefs across shallow shelf areas that seems unlikely: it would require that a species that prefers very shallow coral-reef habitat disperses tens of kilometers across unusable habitat and does so in large enough numbers for appreciable numbers of fish to find their way to tiny, isolated patches of non-coral habitat: the Los Monjes islands are all <1 km in diameter, the Frailes < 2 km, and the Los Testigos all < 5 km in maximum dimension. Larval recruitment to those islands, and to all other similarly isolated islands and reefs on the continental shelf that lack nearby mangroves seems much more likely.

Migration from sites that have nursery habitats to reefs isolated by deep water is even less likely than long-distance trans-shelf movements with larval recruitment the most likely source sustaining populations at such sites. Scarus guacamaia also is now known from sites scattered around the Caribbean that lack mangroves and, in some cases, seagrass beds and are isolated by deep water from the shelves of the nearest land that has such habitat: While there were no Scarus guacamaia in transect surveys made by Scharer et al. (2007) at Mona Island, fishers previously speared this species in shallow water there (M Scharer pers. comm. December 2018), and it has been observed at Monito Island, a 0.5 km diameter islet separated from Mona by 5 km of water ~ 50m deep. It also occurs at nearby Isla Desecho, which lacks both mangroves and seagrasses and is isolated by deep water, 40 km from Puerto Rico, and at Bajo Sico (neither nursery habitat), a submerged bank that rises to within 20m of the surface and is isolated by a 5 km stretch of 190 m-deep water from the shallows of the Puerto Rico shelf, and is 27 km from the nearest mangroves on that island (MT Scharer pers. comm. to DRR, December 2018). Other isolated sites in deep water that lack mangroves and seagrasses and at which this species is now know include Navassa Island and Saba Bank, as well as Swan Island, which lacks mangroves. S. guacamaia is listed as Near Threatened by the IUCN Red List (Choat et al. 2012), due in part to loss of mangrove habitat throughout its geographic range. However, while recruitment to non-mangrove habitats has been established, and is sufficient to maintain a substantial population on a large reef like Alacranes reef, the general significance of such an ability for maintenance of populations of this species are unknown. Large-bodied parrotfishes such as this occur at much lower population densities than small-bodied species and large areas of habitat for both juveniles and adults likely are necessary for maintaining isolated populations. Alacranes reef, which has a surface area of ~ 300 km², provides such an area.

According to Mumby et al. (2015) the extinction of *S. guacamaia* on Glovers Reef (a 350 km² atoll isolated by 20 km of deep water from the shelf edge Barrier Reef of Belize) in the 1970s was most probably due to the removal of mangroves there, although the species also was heavily fished during the mangrove-removal period. This atoll has huge areas of seagrass (>100 km²; Strindberg et al. 2016). However, the atoll has only five tiny (combined area <25 ha) sand cays, some of which once supported mangroves and the total area of mangroves prior to their removal to facilitate human habitation on several of those cays must have been tiny. Censuses in 2007 and 2017 indicate that this species has subsequently remained rare on that reef (A Tewfik, pers. comm. to DRR January 2019). Given what we now know about the ability of the rainbow parrotfish to maintain a population on mangrove-free Alacranes reef by using seagrass and rubble banks as nursery habitat, overfishing of a once self-recruiting population seems more likely than mangrove-loss to account for its demise and subsequent rarity.

To date studies of the relationship between *S. guacamaia* populations and abundance of nursery habitat have focused largely on mangroves as nurseries, and been based on observations alone (Mumby et al. 2004, Machemer et al. 2012, Claydon et al. 2015, and see other studies cited in Table 3). Future studies of nursery habitats of this species necessarily should involve examination and active collections aimed at small juveniles hidden in seagrass beds (cf. Hildebrand et al. 1964), and include observations and collections in other habitats, such as shallow rubble banks now known to be used by small juveniles. Comparison of densities of *S. guacamaia* in areas with and without seagrasses and mangroves are also needed, to assess the population impact of such nursery habitats, taking into account the likely effects of reef-size, and the extent of preferred, emergent habitat for adults on sizes of populations of a large, highly mobile, low density species. Correlational studies focused on the relationship between variation in abundances of mangroves and *S. guacamaia* at the regional level (e.g., Serafy et al. 2015) need to be revisited, incorporating variation in the abundance of both seagrasses and mangroves.

Scarus iseri has been classed as strongly dependent on seagrasses for nursery habitat (Table 3, and see Rocha et al. 2012, Hildebrand et al. 1964). It is ubiquitous, and typically common, on isolated reefs regardless of the presence or absence of both nursery habitats. *Scarus taeniopterus*, which is thought to be somewhat dependent on both mangroves and seagrass beds (Table 3), also is ubiquitous, and often common, on isolated reefs in the region that lack mangroves, and often seagrass beds. These two small parrotfishes evidently maintain significant local populations without mangroves or seagrasses. What habitats they use as nurseries in such situations remains to be determined.

Acanthuridae. Acanthurus chirurgus (Bloch, 1787) has been considered a nursery species that uses other nursery habitats as well as mangroves and seagrasses. This species occurs on all the reefs we considered here, although it is not as common as the other two members of its genus, which are not considered to be nursery species. There is no clear evidence that availability of mangrove or seagrass has any strong influence on its abundance across different reef systems.

Sphyraenidae. *Sphyraena barracuda.* This pelagic species is thought to be mangrove-nursery dependent but also uses seagrass beds (Aiken et al. 2015). It ranges widely across expansive continental shelves, such as that on the west side of Florida, and travels hundreds of kilometers in the open ocean (Hansen and Kerstetter 2015), where it is taken as bycatch by tuna purse-seiners (e.g., Torres-Irineo et al. 2014). Seagrass beds acting as nurseries could support populations on reefs that lack mangroves, including Alacranes reef (see Hildebrand et al. 1964). However, adult dispersal of this large, mobile pelagic fish can account for its occurrence at all isolated locations that lack both nursery habitats, including submerged banks and reefs isolated by deep water from shallow areas containing such habitats (Tables 3–5).

Conclusions about reliance on mangroves and seagrasses as nursery habitats. Even though abundances of the 16 nursery species vary on reefs that have both nursery habitats adjacent to them, patterns of occurrence at isolated shallow reefs that lack mangroves and, sometimes, seagrasses indicate that distributions of only three of 16 nursery species of reef fishes on different reefs are consistent with their being highly dependent on such habitats. Those three are *Haemulon parra*, *H. sciurus*, and *Lutjanus griseus*, which appear to be dependent on seagrass beds as they are lacking on oceanic reefs without such habitat that are also isolated by deep water from immigration. *Lutjanus griseus* evidently has the ability to migrate long distances from shoreline nurseries to isolated reefs on continental shelves. We recognize that the information

on abundances of others of those species that we presented here is relatively crude, and preliminary. Whether the density of populations of the other 13 nursery-species is lower on reefs lacking those nursery habitats remains to be determined, through use of similar methods of quantification of their abundances across a range of reef types. Conclusions of a number of previous studies that have focused on the dependency of Caribbean nursery-species on mangroves or seagrasses are limited in a number of ways: (i) They sometimes have been too narrowly focused on mangroves, rather than including seagrasses and other potential nursery habitats (but see Scharer 2007, 2009, Scharer et al. 2016) and (ii) have not attempted to examine reef systems that lack one or both nursery habitats, particularly reefs that are sufficiently isolated by deep water that immigration to them is highly unlikely (but see Scharer 2007, 2009, Scharer et al. 2016). (iii) All those studies have relied exclusively on observations rather than also employing specimen collections to enable accurate identification of newly recruited fishes (cf. Hildebrand 1964) and quantification of their abundance in different potential nursery habitats. Some reefs have both mangrove and seagrass habitats, others have seagrasses but no mangroves, but none likely have mangroves but not seagrasses as conditions sheltered enough to allow mangrove development invariably also allow seagrass development. This limits our ability to separate the relative influence of each of those two nursery habitats. Finally, the role of macroalgal beds as nursery habitat for Caribbean reef fishes thought to be reliant on mangroves and seagrasses needs evaluation. Eggertsen et al. (2017) found much higher densities of juvenile reef fishes, including some of the "nursery species" discussed here, in macroalgal beds than in beds of Shoal grass adjacent to Brazilian reefs (see also Evans et al. 2014, Tano et al. 2017). On the west Campeche reefs a number of reef fishes commonly seen elsewhere in seagrass beds were found associated with macroalgae: Xyrichtys splendens, Sparisoma atomarium (Poey 1861), S. radians (Valenciennes in Cuvier and Valenciennes 1840), as well as small juveniles of Sphyraena barracuda and Ocyurus chrysurus. Macroalgal beds clearly have the potential to act as suitable habitat for juveniles and adults of a number of reef fishes that commonly use seagrass beds.

While the reefs examined in the present study indicate that none of the 16 nursery species have an obligatory or even strong reliance on mangroves as nursery habitat, and that only a few may be strongly reliant on seagrasses, this does not invalidate the conclusions of previous studies of the importance of those habitats at sites for which the mangrove-nursery hypothesis was developed: Curacao and Bonaire. Those two islands rise abruptly from deep water and have only a very narrow rim of steeply sloping coral reef around their edges, with no sheltered habitat other than in large, peripheral inlets that contain mangroves and seagrasses. It may well be that those inlets provide all or nearly all suitable sheltered nursery habitat for *S. guacamaia* and some of the other nursery species on those islands. However, isolated reefs such as Alacranes reef (and Glover's reef) are very different as it comprises a large, ~ 300 km² oval of reef and shallow lagoon that host large areas of seagrass and shallow rocky substrata, with only a few tiny sand cays (Bello et al. 2005, Purkis et al. 2015). Oceanic islands like Curacao and Bonaire, shallow atolls like Alacranes and Glovers, and large submerged banks

like Saba Bank represent extremes in terms of the absolute and relative abundances of different types of nursery habitat, the usage of which by nursery species may, in most cases, simply reflect their availability.

Acknowledgements

Thanks go to Quetzalli Hernandez, for her highly efficient leadership of logistical preparations and oversight of diving activities during the three expeditions that contributed data to this paper. Georgina Palacios Morales and Xavier Madrigal Guridi for assistance with collecting fishes at Cayo Arcas in 2018. These expeditions were financed by grants to NS from the Harte Research Institute (Biodiversity of the southern Gulf of Mexico) and CONABIO (NE018; Actualización del conocimiento de la diversidad de especies de invertebrados marinos bentónicos de aguas someras (< 50m) del Sur del Golfo de México. A grant from Entropy Foundation also contributed to the costs of the 2018 expedition to Cayo Arcas. Collection of specimens was done under Permiso de Pesca PPF/DGOPA-262-17. Quetzalli Hernandez prepared the satellite images of Cayo Arcas, Triángulo Oeste and Este, and Cayo Arenas. We thank Pix4D (https://www.pix4d. com/) for permission to use individual images to construct the composite images of the four emergent reefs. Ken Marks kindly provided the results of the Agrra fish survey at Swan Island. We thank three reviewers for useful comments on the manuscript.

References

- Aguilar-Perera A, Tuz-Sulub A (2009) Occurrence of the Mardi Gras wrasse, *Halichoeres burekae* (Teleostei: Labridae) in the Alacranes Reef, off northern Yucatán Peninsula. Zootaxa 2298: 64–68.
- Aguilar-Perera A, Quijano-Puerto L, Hernández-Landa RC (2016) Lionfish invaded the mesophotic coral ecosystem of the Parque Nacional Arrecife Alacranes, southern Gulf of Mexico. Marine Biodiversity 47: 15–16. https://doi.org/10.1007/s12526-016-0536-8
- Aguilar-Perera A, Hernández-Landa RC (2017) The rainbow parrotfish (*Scarus guacamaia*) does not depend on mangroves as nursery habitats in the Parque Nacional Arrecife Alacranes, Southern Gulf of Mexico. Marine Biodiversity 47: 13–14. https://doi.org/10.1007/ s12526-016-0491-4
- Aiken KA, Dooley J, Marechal J, Pina Amargos F, Russell B, Singh-Renton S (2015) Sphyraena barracuda (errata version published in 2017). The IUCN Red List of Threatened Species 2015: e.T190399A115319634. https://doi.org/10.2305/IUCN.UK.2015-4.RLTS. T190399A15603115.en
- Belanger CL, Jablonski D, Roy K, Berke SK, Krug AZ, Valentine JW (2012) Global environmental predictors of benthic marine biogeographic structure. PNAS 109: 14046–14051. https://doi.org/10.1073/pnas.1212381109
- Bello PJ, Rios LV, Liceaga CMA, Zetina MC, Cervera CK, Arceo BP, Hernandez NH (2005) Incorporating spatial analysis of habitat into spiny lobster (*Panulirus argus*) stock assessment at Alacranes reef, Yucatán, Mexico. Fisheries Research 73: 37–47. https://doi. org/10.1016/j.fishres.2005.01.013
- Brandl SJ, Goatley CHR, Bellwood DR, Tornabene L (2018) The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs. Biological Reviews 93: 1846–1873. https://doi.org/10.1111/brv.12423
- Chávez H (1966) Peces colectados en el Arrecife T Triángulo Oeste y en Cayo Arenas, Sonda de Campeche, Mexico. Acta Zoologica Mexicana 8: 1–12.
- Chávez E, Tunnell Jr JW, Withers K (2007) Veracruz shelf and Campeche Bank. In: Tunnell Jr JW, Chaez EA, Withers K (Eds) Coral reefs of the southern Gulf of Mexico. Texas A&M Press, College Station, Texas, 41–67.
- Chávez E, Beaver CRK (2007) Reef fish. In: Tunnell Jr JW, Chavez EA, Withers K (Eds) Coral reefs of the southern Gulf of Mexico. Texas A&M Press, College Station, Texas, 102–111.
- Choat JH, Feitosa C, Ferreira CE, Gaspar AL, Padovani-Ferreira B, Rocha LA (2012) *Scarus guacamaia*. The IUCN Red List of Threatened Species 2012: e.T19950A17627624. https://doi.org/10.2305/IUCN.UK.2012.RLTS.T19950A17627624.en
- Claydon JAB, Calosso MC, De Leo GA, Peachey RBJ (2015) Spatial and demographic consequences of nursery-dependence in reef fishes: an empirical and simulation study 2015. Marine Ecology Progress Series 525: 171–183. https://doi.org/10.3354/meps11245
- Cocheret de la Morinière E, Polluxa BJA, Nagelkerken I, van der Velde G (2002) Post-settlement Life Cycle Migration Patterns and Habitat Preference of Coral Reef Fish that use Seagrass and Mangrove Habitats as Nurseries. Estuarine Coastal & Shelf Science 55: 309–321. https://doi.org/10.1006/ecss.2001.0907
- Collette BB, Williams JT, Thacker CE, Smith ML (2003) Shore Fishes of Navassa Island, West Indies: a case study on the need for rotenone sampling in reef fish biodiversity studies. Aqua 6: 89–131.
- del Morales-Flores LF, Tello-Musi JL, Reyes-Bonilla H, Pérez-España H, Martínez-Pérez JA, Horta-Puga G, Velazco-Mendoza LA, Álvarez del Castillo-Cárdenas AA (2013) Systematic checklist and zoogeographic affinities of ichthyofauna from Sistema Arrecifal Veracruzano, Mexico. Revista Mexicana de Biodiversidad 84: 825–846. https://doi.org/10.7550/ rmb.34912
- Dorenbosch M, van Riel MC, Nagelkerken I, van der Velde G (2004) The relationship of reef Fish densities to the proximity of mangrove and seagrass nurseries. Estuarine coastal & shelf Science 60: 37–48. https://doi.org/10.1016/j.ecss.2003.11.018
- Dorenbosch M, Grol MGG, Nagelkerken I, van der Velde G (2006) Seagrass beds and mangroves as nurseries for the threatened Indo-Pacific Humphead wrasse, *Cheilinus undulatus* and Caribbean Rainbow parrotfish, *Scarus guacamaia* Biological Conservation 129: 277–282. https://doi.org/10.1016/j.biocon.2005.10.032
- Dorenbosch M, Verberk WCEP, Nagelkerken I, van der Velde G (2007) Influence of habitat configuration on connectivity between fish assemblages of Caribbean seagrass beds, mangroves and coral reef. Marine Ecology Progress Series 334: 103–116. https://doi. org/10.3354/meps334103

- Eggertsen L, Ferreira CEL, Fontoura L, Kautsky N, Gulstrom M (2017) Seaweed beds support more juvenile reef fish than seagrass beds in a south-western Atlantic tropical seascape. Estuarine, Coastal and Shelf Science 196: 97–108. https://doi.org/10.1016/j.ecss.2017.06.041
- Evans RD, Wilson SK, Field SN, Moore JAY (2014) Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. Marine Biology 161: 599–607. https:// doi.org/10.1007/s00227-013-2362-x
- Flores JS (1992) Vegetacion de Las Islas de La Peninsula De Yucatán: Floristica y Etnobotanica. Etnoflora Yucatanense, Fascículo 4. Universidad Autónoma de Yucatán, Mérida, 100 pp.
- Friedlander AM, Monaco ME, Clark R, Pittman SJ, Beets J, Boulon R, Callender R, Christensen J, Hile SD, Kendall MS, Miller J, Rogers C, Stamoulis K, Wedding L, Roberson K (2013) Fish Movement Patterns in Virgin Islands National Park, Virgin Islands Coral Reef National Monument and Adjacent Waters. NOAA Technical Memorandum NOS NC-COS 172. Silver Spring, MD, 102 pp.
- Garduño M (1988) Distribución de la Ictiofauna ascociada a los Arrecifes del Caribe Mexicano. MSc thesis, Centro de Investigaciones y de Estudios Avanzados el IPN. Unidad Merida, Yúcatan, México.
- Garduño M, Chávez EA (2000) Fish resource allocation in coral reefs of Yucatán Peninsula. Aquatic Ecosystems of Mexico: Status and Scope. In: Munawar M, Lawrence SG, Munawar IF, Malley DF (Eds) Ecovision World Monograph Series 2000. Backhuys, Leiden, 367–381.
- Goatley CHR, González-Cabello A, Bellwood DR (2016) Reef-scale partitioning of cryptobenthic fish assemblages across the Great Barrier Reef, Australia. Marine Ecology Progress Series 544: 271–280. https://doi.org/10.3354/meps11614
- González-Gándara C (2014) Peces de Arrecife Blake, Veracruz, Mexico: Inventario, distribución y afinidades zoogeográficas. Ecosistemas y Recursos Agropecuarios 2: 87–97.
- González-Gándara C, Arias-González JE (2001) Lista actualizada de los peces del arrecife Alacranes, Yucatán, México. Anales del Instituto de Biología, Serie Zoología, Universidad Nacional Autonóma de México 72: 245–258.
- González-Gándara C, de la Cruz Francisco V, Salas Pérez, Dominguez Barradas C (2012) Lista de los peces de Tuxpan, Veracruz, México. Revista Científica UDO Agrícola 12: 675–689.
- González-Gándara C, Lozano Vilano M de L, de la Cruz Francisco V, Dominguez Barradas C (2013) Peces del sistema arrecifal Lobos-Tuxpan, Veracruz, Mexico. Universidad y Ciencia, Trópico Húmido 28: 191–208.
- Green EP, Short FT (2003) World Atlas of Seagrasses. University of California Press, Berkeley, 298 pp.
- Halpern BS (2004) Are mangroves a limiting resource for two coral reef fishes. Marine Ecology Progress Series 272: 93–98. https://doi.org/10.3354/meps272093
- Hansen NR, Kerstetter DW (2015) Habitat use and vertical distribution of the great barracuda Sphyraena barracuda (Edwards 1771) in the western north Atlantic using electronic archival tags. Gulf and Caribbean Research 26: SC4–SC9. https://doi.org/10.18785/gcr.2601.06
- Harborne AR, Nagelkerken I, Wolff NH, Bozec YM, Dorenbosch M, Grol MGG, Mumby PJ (2015) Direct and indirect effects of nursery habitats on coral-reef fish assemblages, grazing pressure, and benthic dynamics. Oikos 125: 957–967. https://doi.org/10.1111/oik.02602

- Hedgepeth JW (1954) Bottom communities of the Gulf of Mexico, U.S. Fishery Bulletin 89: 203–214.
- Hernández-Landa RC, Aguilar-Perera A (2018) Structure and composition of surgeonfish (Acanthuridae) and parrotfish (Labridae: Scarinae) assemblages in the south of the Parque Nacional Arrecife Alacranes, southern Gulf of Mexico. Marine Biodiversity 49: 647–662. https://doi.org/10.1007/s12526-017-0841-x
- Hildebrand HH, Chávez H, Compton H (1964) Aporte al conocimiento de los Peces del Arrecife Alacranes, Yucatán (México). Ciencia (Mexico City) 23: 107–134.
- Hitt S, Pittman SJ, Nemeth RS (2011) Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem Marine Ecology Progress Series 427: 275– 291. https://doi.org/10.3354/meps09139
- Jones DL, Walter JF, Brooks EN, Serafy JE (2010) Connectivity through ontogeny: fish population linkages among mangroves and coral reef habitats. Marine Ecology Progress Series 401: 245–258. https://doi.org/10.3354/meps08404
- Lindeman K, Anderson W, Carpenter KE, Claro R, Cowan J, Padovani-Ferreira B, Rocha LA, Sedberry G, Zapp-Sluis M (2016a) *Lutjanus analis*. The IUCN Red List of Threatened Species 2016: e.T12416A506350. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T12416A506350.en
- Lindeman K, Anderson W, Carpenter KE, Claro R, Cowan J, Padovani-Ferreira B, Rocha LA, Sedberry G, Zapp-Sluis M (2016b) *Lutjanus apodus*. The IUCN Red List of Threatened Species 2016: e.T155152A726254. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS. T155152A726254.en
- Lindeman K, Anderson W, Carpenter KE, Claro R, Cowan J, Padovani-Ferreira B, Rocha LA, Sedberry G, Zapp-Sluis M (2016c) *Lutjanus griseus*. The IUCN Red List of Threatened Species 2016: e.T192941A2180367. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS. T192941A2180367.en
- Lindeman K, Anderson W, Carpenter KE, Claro R, Cowan J, Padovani-Ferreira B, Rocha LA, Sedberry G, Zapp-Sluis M (2016d) *Ocyurus chrysurus*. The IUCN Red List of Threatened Species 2016: e.T194341A2316114. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS. T194341A2316114.en
- Lindeman K, Anderson W, Carpenter KE, Claro R, Padovani-Ferreira B, Rocha LA, Sedberry G (2016e) *Haemulon flavolineatum*. The IUCN Red List of Threatened Species 2016: e.T194418A2333815. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T194418A2333815.en
- Littler DS, Littler MM (2000) Caribbean Reef Plants. An identification guide to the reef plants of the Caribbean, Bahamas, Florida and Gulf of Mexico. Offshore Graphics. Washington DC, 542 pp.
- Logan BW, Harding JL, Ahr WM, Williams JD, Snead RG (1969) Carbonate sediments and reefs, Yucatán shelf, Mexico. American Association of Petroleum Geologists Memoir 11: 1–198.
- Lorda JF, Athíe G, V Camacho I, Daessle LW, Molina O (2019) The relationship between zooplankton distribution and hydrography in oceanic waters of the Southern Gulf of Mexico. Journal of Marine Systems. 192: 28–41. https://doi.org/10.1016/j.jmarsys.2018.12.009
- Machemer EGP, Walter JF III, Serafy JE, Kerstetter DW (2012) Importance of mangrove shorelines for rainbow parrotfish *Scarus guacamaia*: habitat suitability modeling in a subtropical bay. Aquatic Biology 15: 87–98. https://doi.org/10.3354/ab00412

- McClellan DB, Miller GM (2002) Reef fish abundance, biomass, species composition, and habitat characterization of Navassa Island. In: Miller MW (Ed.) Status of reef resources of Navassa Island: cruise report Nov 2002. NOAA Technical Memorandum NMFS-SEF-SC-501, 119 pp.
- Miller MW (2002) Status of reef resources of Navassa Island: cruise report Nov 2002. NOAA Technical Memorandum NMFS-SEFSC-501, 24–42.
- Mumby PJ, Edwards AJ, Arias-González JE, Lindeman KC, Blackwell PG, Gall A, Gorczynska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CCC, Llewellyn G (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427: 533–536. https://doi.org/10.1038/nature02286
- Muñoz RC, Buckel CA, Whitfield PE, Viehman S, Clark R, Taylor JC, Degan BP, Hickerson EL (2017) Conventional and technical diving surveys reveal elevated biomass and differing fish community composition from shallow and upper mesophotic zones of a remote United States coral reef. PLoS ONE 12(11): e0188598. https://doi.org/10.1371/journal.pone.0188598
- Nagelkerken I (2009) Evaluation of nursery function of mangroves and seagrass beds for tropical decapods and reef fishes: patterns and underlying mechanisms. In: Nagelkerken I (Ed.) Ecological Connectivity among tropical coastal ecosystems. Springer, Netherlands, 357–399. https://doi.org/10.1007/978-90-481-2406-0_10
- Nagelkerken I, Dorenbosch M, Verberk WCEP, Cocheret de la Morinière E, van der Velde G (2000a) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. Marine Ecology Progress Series 202: 175–192. https://doi.org/10.3354/meps202175
- Nagelkerken I, van der Velde G, Gorissen MW, Meijer GJ, van't Hof T, den Hartog C (2000b) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuarine, Coastal and Shelf Science 51: 31–44. https://doi.org/10.1006/ecss.2000.0617
- Nagelkerken I, van der Velde G (2003) Connectivity between coastal habitats of two oceanic Caribbean islands as inferred by ontogentic shifts by coral reef fishes. Gulf and Caribbean Research 14: 43–59. https://doi.org/10.18785/gcr.1402.04
- Nagelkerken I, Kleijnen S, Klop T, van den Brand RACJ, Cocheret de la Morniere E, van der Velde G (2001) Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Marine Ecology Progress Series 214: 225–235. https://doi.org/10.3354/meps214225
- Nagelkerken I, Huebert KB, Serafy JE, Grol MGG, Dorenbosch M, Bradshaw JA (2017) Highly localized replenishment of coral reef fish populations near nursery habitats. Marine Ecology Progress Series 568: 137–150. https://doi.org/10.3354/meps12062
- Purkis S, Casini G, Hunt D, Colpaert A (2015) Morphometric patterns in Modern carbonate platforms can be applied to the ancient rock record: Similarities between Modern Alacranes Reef and Upper Palaeozoic platforms of the Barents Sea. Sedimentary Geology 321: 49–69. https://doi.org/10.1016/j.sedgeo.2015.03.001
- Robertson DR, Allen GR (1981) Stegastes mellis (Emery et Burgess, 1974), le juvenile de la Demoiselle Caraïbe Stegastes diencaeus (Jordan et Rutter, 1898). Revue Francaise Aquariologie 7: 109–112.

- Robertson DR, Cramer KL (2014) Defining and Dividing the Greater Caribbean: Insights from the Biogeography of Shorefishes. Plos ONE 9: 1–16. https://doi.org/10.1371/journal.pone.0102918
- Robertson DR, Perez-España H, Nuñez Lara E, Puc Itza F, Simões N (2016a) The fishes of Cayo Arcas (Campeche Bank, Gulf of Mexico): an updated checklist. ZooKeys 640: 139– 155. https://doi.org/10.3897/zookeys.640.10862
- Robertson DR, Simões N, Gutiérrez Rodríguez C, Piñeros VJ, Perez-España H (2016b) An Indo-Pacific damselfish widely established in the southwest Gulf of Mexico: prospects for a wider, adverse invasion. Journal of the Ocean Science Foundation 19: 1–17.
- Robertson DR, Smith-Vaniz WF (2008) Rotenone: an essential but demonized tool for assessing marine fish diversity. Bioscience 58: 165–170. https://doi.org/10.1641/B580211
- Robertson DR, Smith-Vaniz WF (2010) Use of clove oil in collecting coral reef fishes for research. Marine Ecology Progress Series 401: 295–302. https://doi.org/10.3354/meps08374
- Rocha LA, Choat JH, Clements KD, Russell B, Myers R, Lazuardi ME, Muljadi A, Pardede S, Rahardjo P (2012) *Scarus coeruleus*. The IUCN Red List of Threatened Species 2012: e.T190709A17797173. https://doi.org/10.2305/IUCN.UK.2012.RLTS. T190709A17797173.en
- Rocha LA, Collette BB, Grubbs D, Pezold F, Simons J, Caruso J, Carlson J, McEachran JD, Brenner J, Tornabene L, Chakrabarty P, Robertson DR, Claro R, Carpenter KE, Vega-Cendejas M, Camarena-Luhrs T, Espinosa-Perez H, Jelks H, Williams J, Craig MT (2015) *Halichoeres burekae*. The IUCN Red List of Threatened Species 2015: e.T187608A1826968. https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T187608A1826968.en
- Rocha LA, Choat JH, Clements KD, Russell B, Myers R, Lazuardi ME, Muljadi A, Pardede S, Rahardjo P (2012) Scarus iseri. The IUCN Red List of Threatened Species 2012: e.T190732A17782171. https://doi.org/10.2305/IUCN.UK.2012.RLTS.T190732A17782171.en
- Sandin S (2002) Reef fish trophic analysis from Navassa Island: Exploring biotic and anthropogenic factors In: Miller MW (Ed.) Status of reef resources of Navassa Island: cruise report Nov 2002. NOAA Technical Memorandum NMFS-SEFSC-501, 43–56.
- Scharer MT (2006) Mona Island Reef Fish Community Structure and Function for Marine Protected e Area (MPA) Design Distribution of schooling snappers and grunts. Second Annual Symposium for Coastal and Marine Applied Research University of Puerto Rico Sea Grant College Program October 5, 2006, Mayagüez, Puerto Rico, 1–24. https://seagrantpr.org/wp-content/uploads/2014/11/Scharer.pdf
- Scharer MT (2009) Using landscape ecology to describe habitat connectivity for coral reef fishes. PhD thesis, University of Puerto Rico, Mayagüez, 202 pp.
- Scharer MT, Nemeth MI, Appeldoorn RS (2007) Mapping Ontogenetic Habitat Shifts of Coral Reef Fish at Mona Island, Puerto Rico. Proceedings of the 60th Gulf and Caribbean Fisheries Institute November 5–9, 2007 Punta Cana, Dominican Republic: 305–310.
- Serafy JE, Faunce CH, Lorenz JJ (2003) Mangrove shoreline fishes of Biscayne Bay, Florida. Bulletin of Marine Science 72: 161–180.
- Serafy JE, Shideler GS, Araújo RJ, Nagelkerken I (2015) Mangroves enhance reef fish abundance at the Caribbean regional scale. PLoS ONE 10: e0142022. https://doi.org/10.1371/ journal.pone.0142022

- Short FT, Carruthers TJR, van Tussenbroek B, Zieman J (2010a) *Thalassia testudinum*. The IUCN Red List of Threatened Species 2010: e.T173346A6995927. https://doi. org/10.2305/IUCN.UK.2010-3.RLTS.T173346A6995927.en
- Short FT, Carruthers TJR, van Tussenbroek B, Zieman J (2010b) Syringodium filiforme. The IUCN Red List of Threatened Species 2010: e.T173378A7003203. https://doi. org/10.2305/IUCN.UK.2010-3.RLTS.T173378A7003203.en
- Short FT, Carruthers TJR, van Tussenbroek B, Zieman J (2010c) Halodule wrightii. The IUCN Red List of Threatened Species 2010: e.T173372A7001725. https://doi.org/10.2305/ IUCN.UK.2010-3.RLTS.T173372A7001725.en
- Smith-Vaniz WF, Jelks HL, Rocha LA (2006) Relevance of cryptic fishes in biodiversity assessments: A case study at Buck Island Reef National Monument, St. Croix. Bulletin of Marine Science 79: 17–48.
- Strindberg S, Coleman RA, Burns Perez VR, Campbell CL, Majil I, Gibson J (2016) In-water assessments of sea turtles at Glovers Reef Atoll, Belize. Marine Ecology Progress Series 31: 211–225. https://doi.org/10.3354/esr00765
- Tano SA, Eggertsen M, Wikstrom SA, Berkstrom C, Buriyo AS, Halling C (2017) Tropical seaweed beds as important habitats for juvenile fish. Marine and Freshwater Research 68: 1921–1934. https://doi.org/10.1071/MF16153
- Torres-Irineo E, Amande MJ, Gaertner D, Delgado de Molina A, Murua H, Chavance P, Ariz J, Ruiz J, Lezama-Ochoa N (2014) Bycatch species composition over time by tuna purseseine fishery in the eastern tropical Atlantic Ocean Biodiversity and Conservation 23: 1157– 1173. https://doi.org/10.1007/s10531-014-0655-0
- Toller W, Debrot AO, Vermeij MJA, Hoetjes PC (2010) Reef Fishes of Saba Bank, Netherlands Antilles: Assemblage Structure across a Gradient of Habitat Types. PLoS ONE 5(5): 1–13. e9207. https://doi.org/10.1371/journal.pone.0009207
- Tunnell Jr JW (2007) Island Biota. In: Tunnell Jr JW, Chávez EA, Withers K (Eds) Coral reefs of the southern Gulf of Mexico. Texas A&M Press, College Station, Texas, 119–125.
- Tunnell Jr JW, Chávez EA, Withers K (2007) Coral reefs of the southern Gulf of Mexico. Texas A&M Press, College Station, Texas, 194 pp.
- Tunnell Jr JW, Chapman BR (2001) Seabirds of the Campeche Bank Islands, southeastern Gulf of Mexico. Atoll Research Bulletin 482: 1–50.
- Verweij MC, Nagelkerken I, Hans I, Ruseler SM, Mason PRD (2008) Seagrass nurseries contribute to coral reef fish populations. Limnology & Oceanography 53: 1540–1547. https://doi.org/10.4319/lo.2008.53.4.1540
- Weaver DC, Rocha LA (2007) A new species of *Halichoeres* (Teleostei: Labridae) from the western Gulf of Mexico. Copeia 2007: 798–807. https://doi.org/10.1643/0045-8511(2007)7[798:ANSOHT]2.0.CO;2
- Williams JT, Carpenter KE, Van Tassell JL, Hoetjes P, Toller W, Etnoyer P, Smith M (2010) Biodiversity Assessment of the Fishes of Saba Bank Atoll, Netherlands Antilles. PLoS ONE 5(5): 1–37. e10676. https://doi.org/10.1371/journal.pone.0010676
- Zarco-Perelló S, Moreno Mendoza R, Simóes N (2014) Checklist of fishes from Madagascar Reef, Campeche Bank, México. Biodiversity Data Journal 2: e1100. https://doi. org/10.3897/BDJ.2.e1100

Supplementary material I

Figures S1–S10

Authors: D. Ross Robertson, Omar Domínguez-Dominguez, Yareli Margarita López Aroyo, Rigoberto Moreno Mendoza, Nuno Simões

Data type: multimedia

- Explanation note: Figure S1. Satellite image of Cayo Arenas reef complex. The lighthouse is on Isla Arenas, the cay on the western reef. A composite of satellite images by Pix4D, with permission. Notes: C = white center of cloud patch obscuring part of reef. SB = emergent sand bank. Figure S2. Cayo Arenas Island. Abbreviations: P = permanent pond. M = mangrove patch. From a satellite image by Pix4D, with permission. Figure S3. Mangrove patch at Cayo Arenas. Southerly view of patch of small mangroves exposed at low tide on south side of saltwater pond shown in Figure S2. White seabirds resting on rocks around left side of the mangrove patch provide scale for the size of the mangrove bushes. Photograph Quetzalli Hernandez. Figure S4. Satellite view of Triágulo Oeste reef with lighthouse cay. A composite of satellite images by Pix4D, with permission. Figure S5. Satellite view of Triángulo Este reef complex. A composite of satellite images by Pix4D, with permission. Figure S6. Drone view a section of Banco Obispo Norte. Figure S7a,b. Two drone views of Banco Obispo Sur, including 30 m long Isla Mujeres at anchor. Figure **S8**. Drone view of Banco Pera, with the 30 m long Isla Mujeres at anchor. Figure **S9**. Satellite view of the Cayo Arcas reef complex. The lighthouse is on the largest cay. A composite of satellite images by Pix4D, with permission. Figure S10. Mangroves at Cayo Arcas. Young mangrove plants immediately inshore of the reef crest at Cayo Arcas in 2018. Photograph Nuno Simões.
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zookeys.843.33873.suppl1

CHECKLIST



Preliminary report on bycatch fish species collected from the Tokyo Submarine Canyon, Japan

Yusuke Miyazaki¹, Akinori Teramura², Hiroshi Senou³

I Department of Child Studies and Welfare, Shiraume Gakuen College, 1-830 Ogawa-chou, Kodaira, Tokyo 187-8570, Japan 2 Fisheries Laboratory, Graduate School of Agricultural and Life Sciences, The University of Tokyo, 2971-4 Benten-jima, Nishi, Hamamatsu, Shizuoka 431-0214, Japan 3 Kanagawa Prefectural Museum of Natural History, 499 Iryuda, Odawara, Kanagawa 250-0031, Japan

Corresponding author: Yusuke Miyazaki (yukke-bibimba@10.alumni.u-tokyo.ac.jp)

Academic editor: N. Bogutskaya Received 13 December 2018 Accepted 4 April 2019 Pu	ıblished 9 May 2019
http://zoobank.org/18B92F0E-A6BE-4C65-8F90-8C956DE4D21C	

Citation: Miyazaki Y, Teramura A, Senou H (2019) Preliminary report on bycatch fish species collected from the Tokyo Submarine Canyon, Japan. ZooKeys 843: 117–128. https://doi.org/10.3897/zookeys.843.32410

Abstract

An ichthyofaunal list of bycatch species was compiled, the fish captured by bottom gill-nets set at approximately 300 m depth in the Uraga Suido Channel central Japan. Fragmentary ichthyofaunal lists are available for this area; these lists have focused on chondrichthyans or commercial actinopterygians, but voucher specimens have not been prepared for museum storage. An initial list of the fish fauna was compiled with vouchers, and seven species not previously recorded from the channel are reported. Most of these species belong to the Class Actinopterygii; *Apristurus platyrhynchus* (Tanaka, 1909), *Beryx decadac-tylus* Cuvier, 1829, *Hoplostethus japonicus* Hilgendorf, 1879, *Sebastes iracundus* (Jordan & Starks, 1904), *Scalicus amiscus* (Jordan & Starks, 1904), *Atrobucca nibe* (Jordan & Thompson, 1911), and an unidentified species of the eelpout family Zoarcidae. The taxonomic identity of the eelpout and the biogeography of the Uraga Suido Channel are considered. Further research is required to resolve outstanding faunistic issues, but live collections will likely end when the aging fishers who provide the specimens retire. At that point, existing museum collections will become increasingly important for future research. Examination of a collection that may have been previously deposited in the Chiba Prefectural Museum will be essential.

Keywords

deep sea, distributional boundary, Sagami Sea, western Pacific

Introduction

The deep ocean is a frontier for ichthyological exploration. The fish fauna of the deep sea is much less well known than that of shallow coastal zones. Efforts to conserve deep-water fish faunas are essential in the face of threats from anthropogenic disturbance, such as seabed mining (Cuyvers et al. 2018). These efforts are hampered by a dearth of data on deep sea fish diversity.

The Tokyo Submarine Canyon has an unusual hydrography. The shoreward end is located at the mouth of Tokyo Bay (in the narrow sense, defined below). About 31 million people live around the shores of the bay's basin (Tokyo Bay Environmental Information Center 2017). The maximum water depth in the Uraga Suido Channel at 5–7 km offshore is about 700 m (Fig. 1). The canyon drops off rapidly into the Sagami Trough (> 1000 m deep), and then plunges deeper to the Japan Trench (8020 m maximum depth) (Kato et al. 1985).

Knowledge of the fish fauna in the submarine canyon is fragmentary. Obara et al. (2008) compiled a list of chondrichthyans, which are represented by 41 species belonging to eight orders. Some checklists have included deep-sea species of commercial interest, such as the splendid alfonsino *Beryx splendens* Lowe, 1834 and the blackthroat seaperch *Doederleinia berycoides* (Hilgendorf, 1879) (Kohno et al. 2011; Kudo 1997, 2011). The non-commercial ray-finned species occurring in deep water have been little studied, and the few reports available have not provided essential information on voucher specimens, so the records cannot be re-verified.

Data for the ichthyological surveys in the deep waters of the channel have been obtained by examining the bycatch in commercial bottom gill nets. These nets are used to catch the Japanese spider crab, *Macrocheira kaempferi* Temminck, 1836, and the Japanese lobster, *Metanephrops japonicus* (Tapparone-Canefri, 1873). The nets have been deployed by a single fishing boat, the *Chougorou-maru*, since the 1980s. The first author of this report was able to sail on this boat with a TV crew, and was provided with bycatch specimens as the nets were hauled onboard. The specimens captured included some of the first records from the Uraga Suido Channel. Here, we provide a checklist of the fishes of the Tokyo Submarine Canyon with voucher specimens and photographs. We discuss ichthyofaunal issues in the region.

Materials and methods

Definitions of Tokyo Bay and the Sagami Sea

Biogeographical studies of the Uraga Suido Channel have been confused by conflicting definitions of the regions through which it passes, i.e., Tokyo Bay and the Sagami Sea. Some publications have included the channel within Tokyo Bay, while others consider it a component of the Sagami Sea. The broad definition of Tokyo Bay encompasses the Uraga Suido Channel, which includes almost the entire length of the Tokyo Submarine Canyon (Kanou et al. 2010).



Figure 1. Map showing the study site in the eastern Uraga Suido Channel (extending from Cape Tsurugisaki [south-east of the Miura Peninsula] to Cape Sunosaki [south-west of the Boso Peninsula] and from Cape Kan-nonzaki [east of the Miura Peninsula] to Cape Futtsu [west of the Boso Peninsula]). The channel is included within the broad definition of Tokyo Bay (northward from the Uraga-suido Channel) and Sagami Bay (from Cape Irozaki on the southern Izu Peninsula to Cape Nojimazaki, on the southern Boso Peninsula, including Izu-oshima Island). The channel is not included in the narrow definition of Tokyo Bay.

Kudo (1997, 2011) and Kohno et al. (2010) used a broad definition of Tokyo Bay, which is divided into the inner and outer sectors. The inner sector lies to the north of a line from Cape Futtsu to Cape Kan-nonzaki. The outer sector lies south of this line and extends to a southernmost boundary line from Cape Sunosaki to Cape Tsurugisaki (Fig. 1). The outer sector of Tokyo Bay in this broad sense corresponds to the Uraga Suido Channel, which is recognized as a major marine traffic lane and a region for the branding of fish products. However, these definitions are not of biological importance (Furota 1997; Senou et al. 2006). The narrow-definition of Tokyo Bay corresponds to the inner sector.

Senou et al. (2006) compiled an ichthyofaunal list of the Sagami Sea, including the Uraga Suido Channel. We follow this work and use the narrow definition of Tokyo Bay.

Sampling and specimens

The fishing depth was 100–500 m (averaging 200–300 m) below the water surface within the east Tokyo Submarine Canyon, Chiba Prefecture, Japan (Fig. 1; see also Yano et al. 2007; Obara et al. 2008). The fish specimens were provided by two fishers, Mrs Hisao Tejima and Akio Tejima, who operate commercial bottom gill-nets (total 5000 m in length, 1 m in height, and 10 cm mesh size) set on the steep fishing ground (mostly 200–300 m deep). The voyages were undertaken for the production of a TV program series, "Comprehensive Surveys at the Tokyo Bay (original Japanese title: Tokyo-wan Dai-chousa)", during December 2017, and January and March 2018.

Collected specimens were immediately transferred to a mixture of ambient seawater and ice held in insulated boxes. The fishes were later fixed in 10% formalin, and subsequently preserved in 70% ethanol, except for larger specimens more than approximately 1.0 m total length (TL). Color images were captured after about 1–3 hours fixation. The specimens were deposited in the Kanagawa Prefectural Museum of Natural History, Odawara, Japan (KPM-NI), and in the Museum of Marine Science, Tokyo University of Marine Science and Technology, Tokyo, Japan (MTUF-P). Photographic images of the specimens were deposited in the Image Database of Fishes at the Kanagawa Prefectural Museum of Natural History (KPM-NR).

We were not provided with specimens of fishes with commercial value; these we photographed with an Olympus camera on board the vessel or on the dock. In addition to still shots, we also cut frames from video sequences. These images were also registered to the Image Database of Fishes, and some are available online as "FishPix" (see also Miyazaki et al. 2014).

The systematic arrangement of families, scientific names, and standard Japanese names generally follow Nakabo (2013), with a modification (White et al. 2017).

Results and discussion

Based on examinations of our voucher specimens (56 individuals) and the photographic images, we identified 36 species in 25 families and 13 orders (Table 1; Figs 2–5). The collection included rare chondrichthyans, such as the frilled shark *Chlamydoselachus anguineus* Garman, 1884 and the goblin shark *Mitsukurina owstoni* Jordan, 1898, which were previously reported by Yano et al. (2007) and Obara et al. (2008). The four species, *M. owstoni, Lophiomus setigerus* (Vahl, 1797), *Doederleinia berycoides* (Hilgendorf, 1879), and *Eopsetta grigorjewi* (Herzenstein, 1890), were identified from their database photographic images only (Fig. 5); no voucher specimens were deposited in the museums. The compilation included one agnathan, 13 chondrichthyans species (Figs 2, 5), and 21 actin-opterygian species (Figs 3–5). Among the actinopterygians, the family Macrouridae was the most speciose (four species). Other families were represented by one or two species.

We found seven species (Table 1) that had not been included in the previous reports on the fish fauna of the Uraga-suido Channel (Kudo 1997, 2011; Senou et



Figure 2. Photos of the voucher specimens of the agnathan and chondrichthyans species collected from the Uraga Suido Channel, the Sagami Sea, Japan. A MTUF-P 30681: *Eptatretus atami*, 503 mm TL
B KPN-NI 47883: *Chimaera phantasma*, 481 mm TL (tail broken) C KPM-NI 46348: *Hydrolagus mitsukurii*, 315 mm TL (tail broken) D MTUF-P 30716: *Cephaloscyllium umbratile*, 489 mm TL E KPM-NI 46359, *Apristurus platyrhynchus*, 634 mm TL F KPM-NI 46352: *Chlamydoselachus anguineus*, 1258 mm TL G KPN-NI 47884: *Heptranchias perlo*, 910 mm TL H KPM-NI 46346: *Dalatias licha*, 472 mm TL I KPN-NI 47882: *Deania calcea*, 656 mm TL J KPM-NI 46349: *Deania hystricosa*, 844 mm TL K MTUF-P 30717: *Centrophorus atromarginatus*, 453 mm TL L KPM-NI 46356: *Cirrhigaleus barbifer*, 846 mm TL M KPM-NI 46360: *Squalus mitsukurii*, 581 mm TL.

al. 2006; Obara et al. 2008; Kohno et al. 2011): *Apristurus platyrhynchus* (Tanaka, 1909), *Beryx decadactylus* Cuvier, 1829, *Hoplostethus japonicus* Hilgendorf, 1879, *Sebastes iracundus* (Jordan & Starks, 1904), *Scalicus amiscus* (Jordan & Starks, 1904),

Table 1. An ichthyofaunal list with their vouchers collected by our surveys from the seep-sea area (ranges 100–500 m, average 300 m) of the Uraga Suido Channel, the Sea of Sagami, central Japan. The species with an asterisk indicate the first records with voucher(s) from this area.

Order/Family/Species	Standard Japanese name	Voucher number
Myxiniformes		
Myxinidae		
Eptatretus atami (Dean, 1904)	Kuro-nuta-unagi	MTUF-P 30681
Chimaeriformes		
Chimaeridae		
Chimaera phantasma Jordan & Snyder, 1900	Ginzame	KPN-NI 47883
<i>Hydrolagus mitsukurii</i> (Jordan & Snyder, 1904)	Aka-ginzame	KPM-NI 46348; MTUF-P 30679
Lamniformes		
Mitsukurinidae		
Mitsukurina owstoni Jordan, 1898	Mitsukurizame	KPM-NR 193004
Carcharhiniformes		
Scyliorhinidae		
<i>Cephaloscyllium umbratile</i> Jordan & Fowler, 1903	Nanukazame	MTUF-P 30716
Pentanchidae		
Apristurus platyrhynchus (Tanaka, 1909)*	Herazame	KPM-NI 46359, 46365
Chlamydoselachiformes		
Chlamydoselachidae		
Chlamydoselachus anguineus Garman, 1884	Rabuka	KPM-NI 46352, 46354
Hexanchiformes		
Hexanchidae		
Heptranchias perlo (Bonnaterre, 1788)	Edo-aburazame	KPN-NI 47884; MTUF-P 30672
Squaliformes		
Dalatiidae		
Dalatias licha (Bonnaterre, 1788)	Yoroizame	KPM-NI 46346, 46351, 46353
Centrophoridae		
Deania calcea (Lowe, 1839)	Hera-tunozame	KPM-NI 47881, 47882
Deania hystricosa (Garman, 1906)	Sagamizame	KPM-NI 46349 46350 46364
Deanna Nyshricosa (Garman, 1900)	ougannzame	MTUF-P 30671
Centrophorus atromarginatus Garman, 1913	Aizame	MTUF-P 30717
Squalidae		
Cirrhigaleus barbifer Tanaka, 1912	Hige-tsunozame	KPM-NI 46356
Squalus mitsukurii Jordan & Snyder, 1903	Futo-tsunozame	KPM-NI 46360–46363, 47886; MTUF-P 30673
Polymixiiformes		
Polymixiidae		
Polymixia japonica Günther, 1877	Ginmedai	KPN-NI 47867-47869
Gadiformes		
Macrouridae		
<i>Coryphaenoides marginatus</i> Steindachner & Döderlein, 1887	Heri-dara	KPM-NI 46347, 46358, 47880; MTUF-P 30677
Coelorinchus kishinouyei Jordan & Snyder, 1900	Mugura-hige	KPN-NI 47876
Coelorinchus japonicus (Temminck & Schlegel, 1846)	Tõjin	MTUF-P 30678
<i>Coelorinchus tokiensis</i> (Steindachner & Döderlein, 1887)	Miyako-hige	MTUF-P 30680

Order/Family/Species	Standard Japanese name	Voucher number
Lophiiformes		
Lophiidae		
Lophiomus setigerus (Vahl, 1797)	Ankō	KPM-NR 193003
Beryciformes		
Berycidae		
Beryx decadactylus Cuvier, 1829*	Nan'yō-kinme	KPN-NI 47870
Trachichthyidae		
Gephyroberyx japonicus (Döderlein, 1883)	Hashikinme	KPN-NI 47871
Hoplostethus japonicus Hilgendorf, 1879*	Hiuchidai	KPN-NI 47872, 47873; MTUF-P 30682
Perciformes		
Sebastidae		
Helicolenus hilgendorfii (Döderlein, 1884)	Yume-kasago	KPM-NI 47874, 47875
Sebastes iracundus (Jordan & Starks, 1904)*	Ōsaga	KPM-NI 46355
Scorpaenidae		
Scorpaena neglecta Temminck & Schlegel, 1843	Izu-kasago	KPN-NI 47877
Triglidae		
Lepidotrigla guentheri Hilgendorf, 1879	Kanado	KPN-NI 47885
Peristediidae		
Scalicus amiscus (Jordan & Starks, 1904)*	Hige-kihōbō	KPN-NI 47887
Acropomatidae		
Doederleinia berycoides (Hilgendorf, 1879)	Akamutsu	KPM-NR 193002
Malakichthys griseus Döderlein, 1883	Ōme-hata	KPN-NI 47879
Sciaenidae		
Atrobucca nibe (Jordan & Thompson, 1911)*	Kuroguchi	KPM-NI 46357
Pentacerotidae		
Pentaceros japonicus Steindachner, 1883	Tsubodai	MTUF-P 30676
Zoarcidae		
Zoarcidae sp.*	Natsushimachojyagenge	KPN-NI 47888
Gempylidae		
Ruvettus pretiosus Cocco, 1833	Baramutsu	MTUF-P 30674
Pleuronectiformes		
Pleuronectidae		
Tanakius kitaharae (Jordan & Starks, 1904)	Yanagi-mushigarei	KPN-NI 47878; MTUF-P 30675
Eopsetta grigorjewi (Herzenstein, 1890)	Mushi-garei	KPM-NR 193005

Atrobucca nibe (Jordan & Thompson, 1911), and an unidentified species of the eelpout family Zoarcidae (see below). Miya and Aizawa (1995) briefly reported on the ichthyofauna of the same region based on specimens collected with the fishing gear that we used. This work is reported in an abstract for the "Symposium on Taxonomy, Ecology, and Stocks of Elasmobranchs" held at the Ocean Research Institute, University of Tokyo on November 27–28th, 1995. However, neither a species list nor details of voucher specimens were provided, and no publication emerged subsequently. Some of the specimens collected in this 1995 study may have been deposited in the Natural History Museum and Institute, Chiba Prefecture to which they have belonged. Examination of previous collections that may have been deposited in the Chiba Prefectural Museum and other museums will be increasingly important



Figure 3. Photos of the voucher specimens of the actinopterygian species (Polymixiiformes, Gadiformes, and Beryciformes) collected from the Uraga Suido Channel, the Sagami Sea, Japan. A KPN-NI 47868, *Polymixia japonica*, 171 mm SL B KPM-NI 47880, *Coryphaenoides marginatus*, 575 mm TL (tail broken)
C KPN-NI 47876, *Coelorinchus kishinouyei*, 302 mm TL (tail broken) D MTUF-P 30680, *Coelorinchus tokiensis*, 772 mm TL (tail broken) E KPN-NI 47870, *Beryx decadactylus*, 210 mm SL F KPN-NI 47871, *Gephyroberyx japonicus*, 204 mm SL G KPN-NI 47872, *Hoplostethus japonicus*, 140 mm SL.

and essential, because live collections will likely end when the aging fishers who provide the specimens retire.

The fishers who provided our specimens are aging, and no successors are likely to take over their operations. Collections will likely cease when the fishing closes down and hence, museum holdings will become increasingly important for faunistic studies.

The specimen that we identified as *Sebastes iracundus* (Fig. 4B) has a black inner surface in the mouth. Nakabo and Kai (2013) indicated that this coloring is characteristic of *Sebastes flammeus* (Jordan & Starks, 1904). However, other morphological traits, such as the patterns of tooth bands, are indicative of *S. iracundus*. A fishing writer also mentioned the same confusion, that is, it is difficult to identify the two species captured from this area based on the external morphology (Shiina 2019). These two species were regarded as conspecifics by Balanov et al. (2004), but genetic differences between the two entities have been reported subsequently (Orr and Hawkins 2008).



Figure 4. Photos of the voucher specimens of the actinopterygian species (Perciformes, and Pleuronectiformes) collected from the Uraga Suido Channel, the Sagami Sea, Japan. **A** KPN-NI 47875, *Helicolenus hilgendorfii*, 146 mm SL **B** KPM-NI 46355, *Sebastes iracundus*, 531 mm SL **C** KPN-NI 47877, *Scorpaena neglecta*, 158 mm SL **D** KPN-NI 47885, *Lepidotrigla guentheri*, 122 mm SL **E**, **F** KPN-NI 47887, *Scalicus amiscus*, 179 mm SL **G** KPN-NI 47879, *Malakichthys griseus*, 150 mm SL **H** KPM-NI 46357, *Atrobucca nibe*, 348 mm SL I MTUF-P 30676, *Pentaceros japonicus*, 162 mm SL J KPN-NI 47888, Zoarcidae sp., 78 mm SL **K** MTUF-P 30674, *Ruvettus pretiosus*, 536 mm SL **L**, **M** KPN-NI 47878, *Tanakius kitaharae*, 228 mm SL.



Figure 5. Voucher images deposited to the Image Database of Fishes at the Kanagawa Prefectural Museum of Natural History without specimens collected from the Uraga Suido Channel, the Sagami Sea, Japan. **A–D** KPM-NR 193004A–D, *Mitsukurina owstoni* **E, F** KPM-NR 193003A–B, *Lophiomus setigerus* **G** KPM-NR 193002, *Doederleinia berycoides* **H** KPM-NR 193005, *Eopsetta grigorjewi*.

The Uraga Suido Channel is the southern distribution boundary for these species (Nakabo and Kai 2013), and we provide the southernmost record of *S. iracundus*.

The unidentified eelpout (Fig. 4J) in our collections may be a species shown as "Andriashevia natsushimae" by Nishiguchi et al. (2009). However, the name is not available according to Art. 8 of the International Code of Zoological Nomenclature

(International Commission on Zoological Nomenclature 1999). There are inconsistencies in the original description (the number of vertebrae in the holotype) and morphological details are inadequate (Hatooka 2013; Shinohara and Takami 2014). Based on further observations of the external and internal morphology of additional specimens collected from Suruga Bay and Sagami Bay, Shinohara and Takami (2014) reported that the undescribed species probably belongs to an undescribed genus. The taxonomic study of this new entity is ongoing.

Acknowledgements

We deeply appreciate H Tejima, A Tejima, and S Takei for kind cooperation to ride on their fishing boat together and to give us the bycatches for making specimens. We also thank J Matsuzawa, T Nagano, N Kawada, T Kanazawa, R Namiki, K Minomo, K Izumori, T. Moriyama, and other staff belonging to the TV Tokyo, and the Kyodo Television for their help our research and provisions of their movies to register to the image database, H Kohno and A Ishikawa for helping us to process specimens, and T Kudo for comments on ichthyofaunal issues of the Tokyo Bay including the Uraga Suido Channel.

References

- Balanov AA, Kukhlevskiy A, Brykov V (2004) Sebastes flammeus (Jordan et Starks, 1904), a junior synonym of S. iracundus (Jordan et Starks, 1904), with the description of fish from southern part of the Sea of Okhotsk. Journal of Ichthyology 44(1): 1–9.
- Cuyvers L, Berry W, Gjerde K, Thiele T, Wilhem C (2018) Deep Seabed Mining: A Rising Environmental Challenge. IUCN and Gallifrey Foundation, Gland, Switzerland, 74 pp. https://doi.org/10.2305/IUCN.CH.2018.16.en
- Furota T (1997) Ecosystem and environmental status in Tokyo Bay. In: Numata M, Furota T (Eds) Biology in Tokyo Bay. Tsukiji Shokan, Tokyo, 2–23. [in Japanese]
- Hatooka K (2013) Zoarcidae. In: Nakabo T (Ed.) Fishes of Japan with Pictorial Keys to the Species (3rd edn). Tokai University Press, Hiratsuka, 1220–1237, 2076–2082. [in Japanese]
- ICZN (1999) International Code of Zoological Nomenclature, (4th edn). International Trust for Zoological Nomenclature, London, 306 pp.
- Kato S, Nagai T, Tamaki M, Kondo T, Tomiyasu Y, Kato G, Muneda K, Asada A (1985) Submarine topography of the eastern Sagami Trough to the triple junction. Report of Hydrographic Researches 20: 1–24. [in Japanese with English abstract]
- Kohno H, Yokoo T, Kanou K (2011) How many species recorded from the bay? In: Kohno K, Kanou K, Yokoo T (Eds) A Photographic Guide to the Fishes in Tokyo Bay. Heibonsha, Tokyo, 31–36, 331–340, 358–360. [in Japanese]
- Kudo T (1997) Fish. In: Numata M, Furota T (Eds) Biology in Tokyo Bay. Tsukiji Shokan, Tokyo, 115–142. [in Japanese]

- Kudo T (2011) Fish. In: The Research Committee of the Tokyo Bay (Ed.) Tokyo Bay: the Restoration for the Relationship between Human and Nature. Koseisha-kouseikaku, Tokyo, 157–161. [in Japanese]
- Miya M, Aizawa M (1995) Elasmobranchs of the Tokyo Submarine Canyon. Report of Japanese Society for Elasmobranch Studies 32: 33. [in Japanese]
- Miyazaki Y, Murase A, Shiina M, Naoe K, Nakashiro R, Honda J, Yamaide J, Senou H (2014) Biological monitoring by citizens using Web-based photographic databases of fishes. Biodiversity and Conservation 23(9): 2383–2391. https://doi.org/10.1007/s10531-014-0724-4
- Nakabo T [Ed.] (2013) Fishes of Japan with Pictorial Keys to the Species, Third Edition. Tokai University Press, Hiratsuka, 2432 pp. [in Japanese]
- Nakabo T, Kai Y (2013) Sebastidae. In: Nakabo T (Ed.) Fishes of Japan with Pictorial Keys to the Species (3rd edn). Tokai University Press, Hiratsuka, 668–681, 1933–1938. [in Japanese]
- Nishiguchi Y, Miwa T, Kubota S, Taru M, Okada M (2009) Characterization of Andriashevia natsushimae, a new species of eelpout (Pisces, Perciformes: Zoarcidae) from Sagami Bay, Japan, and its phylogenic status as inferred from 16S rRNA. Journal of Japanese Society for Extremophiles 8(1): 20–23. https://doi.org/10.3118/jjse.8.20
- Obara G, Jo K, Yamagami K, Kojima T, Taniguchi T (2008) Species composition of chondrichthyans in the Tokyo Submarine Canyon. Report of Japanese Society for Elasmobranch Studies 44: 8–20. [in Japanese with English abstract]
- Orr JW, Hawkins S (2008) Species of the rougheye rockfish complex: resurrection of *Sebastes melanostictus* (Matsubara, 1934) and a redescription of *Sebastes aleutianus* (Jordan and Evermann, 1898) (Teleostei: Scorpaeniformes). Fishery Bulletin 106(2): 111–134.
- Senou H, Matsuura K, Shinohara G (2006) Checklist of fishes in the Sagami Sea with zoogeographical comments on shallow water fishes occurring along the coastlines under the influence of the Kuroshio Current. Memoirs of the National Science Museum, Tokyo 41: 389–542.

Shiina Y (2019) Beni-akō 1 [the fishes called "Beni-akō"]. Tsuri-Joho 42(1): 92–93. [in Japanese]

- Shinohara G, Takami M (2014) Taxonomy and morphology of the zoarcoid fish named "Natsushima-choja-genge." Advance Abstracts for 47th Annual Meeting of the Ichthyological Society of Japan 2014: 41. [in Japanese]
- Tokyo Bay Environmental Information Center (2017) The Environment around the Tokyo Bay. http://www.tbeic.go.jp/kankyo/. [Accessed on 30 August 2018; in Japanese]
- White WT, Mana RR, Naylor GJP (2017) Description of a new species of deepwater catshark *Apristurus yangi* n. sp. (Carcharhiniformes: Pentanchidae) from Papua New Guinea. Zootaxa 4320: 25–40. https://doi.org/10.11646/zootaxa.4320.1.2
- Yano K, Miya M, Aizawa M, Noichi T (2007) Some aspects of the biology of the goblin shark, *Mitsukurina owstoni*, collected from the Tokyo Submarine Canyon and adjacent waters, Japan. Ichthyological Research 54(4): 388–398. https://doi.org/10.1007/s10228-007-0414-2

RESEARCH ARTICLE



An unknown collection of lizards from Afghanistan

Daniel Jablonski¹, Aleksandar Urošević², Marko Andjelković², Georg Džukić²

l Department of Zoology, Comenius University in Bratislava, Ilkovičova 6, Mlynská dolina, 842 15 Bratislava, Slovakia **2** University of Belgrade, Institute for Biological Research "Siniša Stanković", Bulevar Despota Stefana 142, 11000 Belgrade, Serbia

Corresponding author: Daniel Jablonski (daniel.jablonski@balcanica.cz)

Academic editor: Aaron Bauer Received 31 August 2018 Accepted 4 March 2019 Published 9 May	2019
Citation: Jablonski D. Urošević A. Andielković M. Džukić G (2019) An unknown collection of lizards	from

Citation: Jablonski D, Urošević A, Andjelković M, Džukić G (2019) An unknown collection of lizards from Afghanistan. ZooKeys 843: 129–147. https://doi.org/10.3897/zookeys.843.29420

Abstract

Afghanistan is a herpetologically understudied country with few published papers since the end of "Afghanistan's Golden Age" from the 1930s to the 1970s. Although a detailed checklist of the herpetofauna of the country, based on exploration of herpetodiversity using biodiversity archives, has been published recently, there still exist additional historical data that have not been considered. This is the case for a so far unknown collection of lizards from Afghanistan deposited in the herpetological collection of the Institute for Biological Research "Siniša Stanković at the University of Belgrade, Belgrade, Serbia. The material comes from field research conducted in 1972 and contains 27 specimens in seven lizard genera representing four families (Agamidae, Gekkonidae, Lacertidae, Scincidae). This historical collection was examined and basic morphometric data, field data, and photographs are provided, comparing the distributional data with published datasets. Updated species distribution maps reveal new locality or province records and an important range extension for *Eurylepis taeniolata* Blyth, 1854 which represents the northernmost record for this species in Afghanistan. In addition, one further distribution record for the *Bufotes viridis* (Laurenti, 1768) complex from the same research trip is noted.

Keywords

Biogeography, *Bufotes*, Central Asia, faunistics, historical data, museum collection, new records, Reptilia, Squamata

Introduction

A transition zone between the Palearctic and Oriental faunas, a species hotspot for some amphibians and reptiles (Hynobiidae, Agamidae, Lacertidae, Colubridae), areas that never been zoologically explored, and unknown or taxonomically unresolved species; these reasons make Afghanistan one of the most important herpetological regions of the world (Leviton and Anderson 1970, Clark 1990, Böhme and Szczerbak 1991, Wagner et al. 2016). On the other hand, 40 years of war have made the country one of the most inaccessible in the world, where current zoological or herpetological research is almost completely non-existent. This is evident in the published research related to this country (see Nahif 1986). Since the end of Afghanistan's so-called "Golden Age" in the mid-1970s, only a few papers on its herpetofauna have been published (Böhme and Szczerbak 1991, Clark 1992, Kuch 2004, Moravec et al. 2006, Wagner et al. 2016, Jablonski and Lesko 2018). However, most of these papers are related to field research trips from the period between the 1950s and 1970s.

Wagner et al. (2016) presented a summary of most of the known material from Afghanistan in the form of an up-to-date checklist with distributional data and maps for all species based on data from biodiversity archives. According to Wagner et al. (2016), the herpetofauna of Afghanistan comprises 116 species (118 with subspecies) belonging to 58 genera and 21 families. Though the authors were consistent and examined material stored in museum and private collections, there still exist additional historical data or material not incorporated into the checklist. These include collections that were or are unknown for different reasons (forgotten personal collections, unclassified or noncatalogued collections, etc.). This is the case for the recently reported upon herpetological collection of the Institute for Biological Research "Siniša Stanković" of the University of Belgrade, Belgrade, Serbia (Džukić et al. 2017). This collection currently contains 8213 specimens originating from 23 countries. Apart from assigning collection numbers to the specimens, there have not been, until now, any systematic efforts to sort and catalogue the collection. This is why the original collection of lizards from a field trip conducted in Afghanistan during 1972 has not been previously studied. The field trip results and collected specimens were only mentioned once at the national congress of former Yugoslavia (Džukić and Vasić 1974) without any details published in the proceedings.

Because distribution data relating to the herpetofauna of Afghanistan are very important from a biogeographical point of view and comparative material from this country is rare, we have evaluated particular species and specimens stored in the Belgrade collection and compared them with information and distribution data from Wagner et al. (2016).

Material and methods

This material comes from a field trip to Afghanistan that was conducted between 3 and 25 August 1972 by Vojislav Vasić. The specimens of herpetofauna were col-

lected primarily during different ornithological field trips inside the country (see Vasić 1974; this work is missing in the bibliographical overview related to zoological research in Afghanistan presented by Nahif 1986). Overall, 27 specimens in seven genera are discussed. The material was originally determined to the subspecies level according to the keys of Schmidtler and Schmidtler (1969) and Leviton and Anderson (1970). Together with lizards, an additional record of the Bufotes viridis Laurenti, 1768 complex was mentioned (Džukić and Vasić 1974), but the voucher specimens have, unfortunately, been lost. We identified this collection to the species level and available material was coordinated with the classification of Wagner et al. (2016). Localities and dates of collection for each specimen were noted using the original labels. The material is currently in the collection of the Institute for Biological research "Siniša Stanković" preserved in 75% ethanol. Some specimens had previously been kept in the freezer or stored in formaldehyde and were recently transferred to 75% ethanol. All material is stored in labelled single-species glass jars grouped by the country and region of origin in order to facilitate their cataloguing and future work with the collection. During 2011 and 2017 the material was revised and this collection is a result of this work (Džukić et al. 2017). Whereas this collection from Afghanistan is not large and information regarding to the fauna of the country is important, all specimens were examined morphologically and photographed in detail. We examined ten basic morphological characters following Cameron et al. (2013): snout-to-vent length (SVL), body length (BL), tail width (TW), tail length (TL), jaw width (JW), jaw length (JL), fore-limb length left (FLL L), fore-limb length right (FLL R), hind-limb length left (HLL L), hind-limb length left (HLL R). Measurements were taken with a digital caliper to the nearest 0.1 mm. Morphometric data for all specimens are presented in Table 1. We have taken photos of the ventral and dorsal aspects of the specimens, as well as of details of the cloaca, the pileus, and the left and right sides of the head (see Results and Suppl. material 1). All available data relevant to each record (name of the locality, coordinates, sex, date, type of habitat) were noted and are presented. We reviewed locality data presented by Wagner et al. (2016) and made updated maps for particular species using QGIS software (2018).

Results and discussion

REPTILIA Agamidae

Paralaudakia badakhshana (Anderson & Leviton, 1969), Badakhshana Rock Agama

Fig. 1, Suppl. material 1: Figs S1-S3

Originally identified as Agama badakhshana.

Voucher No.	Specimen No.	Species	SVL	BL	ΤW	TL	JW	JГ	FLLL	FLLR	HLLL	HLL R
167	Ι	Mesalina watsonana	45.18	36.96	5.46	61.84	7.20	11.63	8.87	8.88	14.67	14.65
168	I	Eurylepis taeniolata	78.55	66.85	6.98	110.40	8.86	14.21	8.89	8.91	12.31	12.33
169	I	Eutropis dissimilis	82.59	65.08	9.27	I	12.05	19.72	13.93	14.02	16.12	16.09
753	753/1	Paralaudakia badakhshana	77.43	61.35	10.31	101.66	15.16	20.28	10.76 + 9.56	10.64 + 9.86	17.20 + 16.54	16.20 + 16.04
753	753/2	Paralaudakia badakhshana	68.78	51.34	9.00	I	15.38	20.09	10.98 + 9.52	10.12 + 9.52	18.04 + 18.13	18.08 + 18.05
753	753/3	Paralaudakia badakhshana	73.23	57.89	10.90	125.36	16.74	19.62	12.16 + 10.51	12.19 + 10.52	17.16 + 16.99	16.81 + 17.13
753	753/4	Paralaudakia badakhshana	80.50	63.41	12.20	137.35	18.30	20.43	13.77 + 10.94	13.16 + 10.87	20.50 + 17.43	20.53 + 17.38
622	779/1	Ablepharus lindbergi	48.46	37.29	4.18	60.14	5.54	8.56	7.50	7.52	10.42	10.38
622	779/2	Ablepharus lindbergi	45.38	35.53	5.04	I	6.52	10.24	7.81	7.85	12.29	12.27
795	795/1	Tenuidactylus turcmenicus	62.30	46.93	6.96	I	12.86	17.23	8.77 + 9.88	8.62 + 9.89	14.22 + 12.67	13.80 + 12.12
795	795/2	Tenuidactylus turcmenicus	62.93	46.89	7.26	89.58	15.30	18.07	8.12 + 10.26	8.41 + 10.70	14.36 + 13.15	14.48 + 13.46
795	795/3	Tenuidactylus turcmenicus	39.99	30.63	3.86	52.00	9.02	12.15	6.31 + 7.06	6.25 + 7.07	9.31 + 8.49	9.42 + 8.48
795	795/4	Tenuidactylus turcmenicus	58.33	43.60	5.15	79.44	12.40	16.18	7.52 + 10.02	7.59 + 10.12	14.25 + 12.56	14.20 + 12.52
795	795/5	Tenuidactylus turcmenicus	64.17	47.41	6.70	76.07	13.03	16.62	7.48 + 11.06	7.46 + 10.90	15.36 + 13.30	15.19 + 13.62
795	795/6	Tenuidactylus turcmenicus	56.03	41.25	5.16	75.27	11.87	15.43	6.36 + 8.94	6.19 + 8.90	12.15 + 13.13	12.10 + 13.19
795	719517	Tenuidactylus turcmenicus	48.05	35.38	4.63	I	10.71	14.04	6.24 + 8.23	6.34 + 8.28	12.72 + 11.21	12.82 + 11.29
795	795/8	Tenuidactylus turcmenicus	47.87	36.93	4.68	I	10.73	13.64	6.26 + 7.88	6.20 + 7.87	10.85 + 10.47	10.80 + 10.32
795	795/9	Tenuidactylus turcmenicus	64.21	47.95	5.99	90.76	12.68	16.98	8.96 + 10.84	8.86 + 10.22	16.60 + 14.08	16.25 + 14.04
795	795/10	Tenuidactylus turcmenicus	55.53	41.65	4.90	I	11.04	15.27	7.43 + 8.51	7.46 + 8.48	12.79 + 11.16	12.46 + 11.43
887	887/A	Trapelus megalonyx	68.64	50.94	9.30	75.89	17.22	19.89	9.82 + 10.31	9.87 + 12.07	15.80 + 16.91	15.24 + 15.89
887	887/B	Trapelus megalonyx	34.18	22.03	3.97	41.89	9.58	11.01	5.63 + 5.62	5.30 + 5.58	8.08 + 8.72	8.63 + 8.62
912	912/1	Paralandakia cancasia	131.06	104.55	17.33	I	22.58	32.77	18.10 + 19.18	18.45 + 19.20	30.41 + 27.43	31.07 + 27.93
912	912/2	Paralandakia cancasia	88.21	67.29	12.43	137.44	19.56	24.84	13.88 + 14.38	13.66 + 14.34	24.33 + 22.63	23.21 + 21.53
912	912/3	Paralandakia cancasia	138.74	110.38	17.83	158.23	28.78	35.81	22.34 + 17.95	21.46 + 17.05	31.21 + 29.24	31.75 + 29.35
912	912/4	Paralaudakia caucasia	103.70	80.87	15.07	I	22.08	28.87	18.17 + 14.75	17.55 + 15.00	27.70 + 25.89	26.48 + 25.80
912	912/5	Paralandakia cancasia	90.99	69.73	14.00	I	18.25	24.29	15.12 + 13.22	15.13 + 13.28	25.32 + 21.78	24.71 + 21.69
912	912/6	Paralaudakia caucasia	117.96	95.41	18.25	I	25.05	31.52	18.91 + 15.38	18.68 + 15.94	31.96 + 28.50	31.58 + 28.70

Material. Four adult specimens: 753/1 (F), 3 August 1972, Bamyan town (= Bamijan; original name on label), Bamyan, 34°48'1.65"N, 67°49'16.09"E, (desert with rocky outcrops); 753/2 (M), 753/3 (M), 753/4 (M), 4 August 1972, Azhdar-e Surkhdar (= Davolja dolina original name on label), Bamyan, 34°49'57.68"N, 67°46'22.45"E, (desert with rocky outcrops).

Distribution in Afghanistan. Mainly central parts of the Hindu Kush range, with extended records in Badakhshan (including the Wakhan corridor) and Balkh provinces. This species is currently known from the provinces of Badakhshan, Balkh, Bamyan, Ghazni, Kabul, Parwan, and Wardak (Fig. 2; Wagner et al. 2016). The record "Salang Pass, N of, road to Pulikumri [= Pol-e Khomri, Prov. Baghlan] (USNM 194973-76)" presented by Wagner et al. (2016; p. 417) is not georeferenced but will probably correspond geographically with record from "Salang Pass [Kabul Prov., 3000 m] (ZFMK 5377-81)". Both our records are new localities for the species (Fig. 2).

Paralaudakia caucasia (Eichwald, 1831), Caucasian Agama

Fig. 3, Suppl. material 1: Figs S4–S8

Originally identified as *Agama caucasica*.

Material. Six adult specimens: 912/1 (?) and 912/2 (?), 12 August 1972, Qala-e-Naw (= Kala-I-Nav – original name on label), Badgis, 34°57'58.97"N, 63°8'41.85"E, (desert with loess profiles); 912/3 (?) and 912/4 (?), 8 August 1972, Jam (= Džam), Ghor, 34°23'45.51"N, 64°30'57.52"E, (gorge with large boulders and rocks); 912/5 (probably F) and 912/6 (M), 16 August 1972, Takht-e Rostam (=Takt - I - Rosten, Samangan), Samangan, 36°14'47.43"N, 68°1'12.29"E, (rocky desert).

Distribution in Afghanistan. This species has a wide distribution range from the northwestern to the southeastern parts of the country, including northern Badakhshan. It is currently known from the provinces of Badakhshan, Badgis, Baglan, Balkh, Bamyan, Ghazni, Ghor, Herat, Kabul, Khost, Logar, Nangarhar, Paktia, Paktika, Panjshir, Takhar, and Wardak (Fig. 4; Wagner et al. 2016). The following records presented by Wagner et al. (2016; p. 472) are not georeferenced: "Bamiyan, NW of Kabul (MCZ R-97297-98)"; "40 mi S Characharan (CAS 147465)"; "Masdjed-Tchoubi (MZLU L959/3051)"; "above Pagham (Smith 1940: 384; probably BMNH 1940.3.1.18)". Our specimens document new locality records for the species and include the first species record for Samangan Province (Fig. 4).

Trapelus megalonyx Günther, 1864, Afghan Ground Agama

Fig. 5, Suppl. material 1: Fig. S9

Originally identified as Agama ruderata megalonyx.



Figure 1. The specimen of *Paralaudakia badakhshana* no. 753/1 from Bamyan town, Bamyan. Other specimens are presented in Suppl. material 1.



Figure 2. Distribution of *Paralaudakia badakhshana* in Afghanistan – white dots are from Wagner et al. (2016), red dots from this study: I Bamyan **2** Azhdar-e Surkhdar.



Figure 3. The specimen of *Paralaudakia caucasia* no. 912/5 from Takht-e Rostam, Samangan. Other specimens are presented in Suppl. material 1.



Figure 4. Distribution of *Paralaudakia caucasia* in Afghanistan – white dots from Wagner et al. (2016), red dots from this study: I Qala-e-Naw, Badgis **2** Jam, Ghor **3** Tasht-e Rostam, Samangan.



Figure 5. The specimen of *Trapelus megalonyx* no. 887/A from Shawarkhil, Kabul. The second specimen is presented in Suppl. material 1.



Figure 6. Distribution of *Trapelus megalonyx* in Afghanistan – white dots from Wagner et al. (2016), red dots from this study: **I** Kabul – Guldara, Kabul **2** Shawarkhil, Kabul.

Material. One adult and one juvenile specimen: 887/A (F), 21 August 1972, Shawarkhil (=Šivaki, Kabul), Kabul 34°48'3.02"N, 69°9'26.03"E, (habitat data not available); 887/B (?), 21 August 1972, Kabul – Guldara (= Kabul, Guldara), Kabul 34°45'08.89"N, 68°59'23.58"E, (rocky desert).

Distribution in Afghanistan. This species is known mainly from south-eastern parts of the country in the provinces of Baglan, Ghazni, Kabul, Kandahar, Kapisa, Logar, Nangarhar, Uruzgan, and Wardak (Fig. 6; Wagner et al. 2016). One record from Fayzabad (Badakhshan) is not marked on the map of Wagner et al. (2016: p 481 and pl 5, p 541). Both new records document additional localities for the species (Fig. 6).

Gekkonidae

Tenuidactylus turcmenicus (Szczerbak, 1978), Turkmenian Thin-Toed Gecko Fig. 7, Suppl. material 1: Figs S10–S18

Originally identified as Cyrtodactylus fedtschenkoi.

Material. Nine adult and one subadult specimens: 795/1 (F), 795/2 (M), 795/3 (?) subadult, 795/4 (F), 13 August 1972, Maymana, Faryab (= Farjab, Maymana), 35°54'54.99"N, 64°46'30.01"E, (walls of the houses in the village); 795/5 (M), 795/6 (F), 795/7 (M), 795/8 (F), 795/9 (M), 795/10 (F), 16 August 1972, Takht-e Rostam, Samangan (Takt - I - Rosten, Samangan), 36°14'47.43"N, 68°1'12.29"E, (small cave 3 km from Samangan town).

Distribution in Afghanistan. Mainly northern parts of the country, from approximately Bala Morgab to Kunduz (Fig. 8; Wagner et al. 2016). This species is known from the provinces of Balkh, Farah, Herat, Jowzjan, Kunduz, and Takhar. Wagner et al. (2016: 490) also mentioned the record "Seistan [Faizabad Prov.] (ZMUC R-34128)". This record is probably incorrect as there is not a Faizabad Prov. in Afghanistan. The city Faizabad (Fayzabad) is in Badakhshan Prov. (eastern Afghanistan). Moreover, the coordinates provided by authors in the Appendix 1 are the same as for locality "Seistan [= Sistan area near Iran border]" on p 556 (western Afghanistan). Its potential distribution in Badakhshan needs further clarification. On the other hand, Wagner et al. (2016: 490) presented the record "Kouh-Akhour near Farah (NMW 15879)" which is not shown on their map, but represents the southern- and easternmost locality of the species in Afghanistan (see map in Fig. 8 and compare it with the species map in Wagner et al. 2016: pl 6, p 542). This range extension needs further clarification. Both records reported here represent new locality records for the species and first records for the provinces of Faryab and Samangan (Fig. 8).



Figure 7. The specimen of *Tenuidactylus turcmenicus* no. 795/5 from Takht-e Rostam, Samangan. Other specimens are presented in Suppl. material 1.



Figure 8. Distribution of *Tenuidactylus turcmenicus* in Afghanistan – white dots from Wagner et al. (2016), red dots from this study: I Maymana, Faryab 2 Takht-e Rostam, Samangan.

Lacertidae

Mesalina watsonana (Stoliczka, 1872), Persian Long-Tailed Desert Lizard Fig. 9

Originally identified as *Eremias guttulata*.

Material. One adult specimen: 167 (M), 21 August 1972, Kabul – Guldara, Kabul (= Kabul, Guldara), 34°45'08.89"N, 68°59'23.58"E, (rocky desert).

Distribution in Afghanistan. A common species with a number of records mainly from southern Afghanistan below the Hindu Kush Range. It is currently known from the following provinces: Badakhshan, Farah, Ghazni, Ghor, Helmand, Herat, Kabul, Kandahar, Khost, Logar, Nangarhar, Paktia, Paktika, Parwan, Uruzgan, Wardak, and Zabul (Wagner et al. 2016 and Fig. 10). Two localities mentioned by Wagner et al. (2016: 498): "40 km NE of Kandhar, on Tarnak River (CAS 90757-60" and "Mil-Karez, Pol-Mil (MZLU L958/3230)" are not presented with coordinates. Therefore, they are not included in the map (Fig. 10). Guldara is an additional record for the species, whereas this lizard is known from many of records in Kabul Province (Fig. 10).

Scincidae

Ablepharus lindbergi Wettstein, 1960, Lindberg's Snake-Eyed Skink

Fig. 11, Suppl. material 1: Fig. S19

Originally identified as Ablepharus bivittatus lindbergi.

Material. Two adult specimens: 779/1 (?), 4 August 1972; 779/2 (?), 5 August 1972, Band-e Amir, (= Band I Amir), Bamyan, 34°50'1.51"N, 67°12'58.35"E, (arid soil desert with vegetation).

Distribution in Afghanistan. Scattered localities in the western and central Hindu Kush and Shinkay Hills. This species is currently known from the provinces of Baghlan, Bamyan, Ghazni, Herat, Paktika and Uruzgan (Wagner et al. 2016 and Fig. 12). The following localities presented by Wagner et al. (2016; p. 499) were not georeferenced by those authors and they are not shown on the map (Fig. 12): "Kotale-sh-tu [Maidan Prov., western Behsud, 2000 m] (ZFMK 8664)"; "Masdjed, Tohoubi (MZLU L959/3044)"; Tshomay [Maidan Prov., western Behsud, 2000 m] (ZFMK 8663)". The locality presented here is a new record although this lizard was previously known from this region and from the province (Fig. 12).



Figure 9. The specimen of Mesalina watsonana no. 167 from Kabul - Guldara, Kabul.



Figure 10. Distribution of *Mesalina watsonana* in Afghanistan – white dots from Wagner et al. (2016), red dot from this study: Kabul – Guldara, Kabul.



Figure 11. The specimen of *Ablepharus lindbergi* no. 779/1 from Band-e Amir, Bamyan. The second specimen is presented in Suppl. material 1.



Figure 12. Distribution of *Ablepharus lindbergi* in Afghanistan – white dots from Wagner et al. (2016), red dot from this study: Band-e Amir, Bamyan.

Eurylepis taeniolata Blyth, 1854, Yellow-bellied Mole Skink Fig. 13

Originally identified as *Eumeces taeniolatus*.

Material. One adult specimen: 168 (probably M), 16 August 1972, Takht-e Rostam (= Takt - I – Rosten, Samangam), Samangan, 36°14'47.43"N, 68°1'12.29"E, (rocky desert).

Distribution in Afghanistan. The species is known from three localities in southern and south-eastern parts of the country, and from one locality in the northwestern part of the country (provinces of Badghis, Kandahar, Khost, and Nangarhar; Wagner et al. 2016 and Fig. 14). One locality ("Tajan River" probably from Herat province) originating from Leviton and Anderson (1970) and given also by Wagner et al. (2016), is not georeferenced and is not included in our map (Fig. 14). The locality presented here is a new record for the species and the first record for Samangan Province in northern Afghanistan. It is also the northernmost species record for Afghanistan, located more than 300 airline km from the Nangarhar record (Somarkhel) and more than 400 km from the Badghis record (Bala Murghab, Fig. 14; see also Wagner et al. 2016).

Eutropis dissimilis (Hallowell, 1857), Striped Grass Skink

Fig. 15

Originally identified as Mabuya dissimilis.

Material. One adult specimen: 169 (probably M), 25 August 1972, Jalalabad – Hadda (= Hada, Džalalabad), Nangarhar, 34°21'54.86"N, 70°28'34.37"E, (grassy patch in the desert).

Distribution in Afghanistan. The species is known only from three localities in the southeastern part of the country in Nangarhar Province (Wagner et al. 2016 and Fig. 16). Our locality is a new locality record for the species, although it is known from the vicinity of Jalalabad and in Nangarhar Province (Fig. 16).

AMPHIBIA Bufonidae

Bufotes viridis (Laurenti, 1768) complex, Green Toad Fig. 17

Originally identified as: Bufo raddei.

Material. Two voucher specimens that are currently not found in the museum collection were collected on 3 August 1972 in the vicinity of Bamyan town (= Bamijan), 34°48'1.65"N, 67°49'16.09"E, (irrigation canals near the town). The specimens were identified as *Bufo raddei* based on the morphometric characters, according to Schmidtler and Schmidtler (1969).



Figure 13. The specimen of *Eurylepis taeniolata* no. 168 from Takht-e Rostam, Samangan.



Figure 14. Distribution of *Eurylepis taeniolata* in Afghanistan – white dots from Wagner et al. (2016), red dot from this study: Takht-e Rostam, Samangan.



Figure 15. The specimen of Eutropis dissimilis no. 169 from Jalalabad – Hadda, Nangarhar.



Figure 16. Distribution of *Eutropis dissimilis* in Afghanistan – white dots from Wagner et al. (2016), red dot from this study: Jalalabad – Hadda, Nangarhar.


Figure 17. Distribution of all species forming *Bufotes viridis* complex in Afghanistan – white symbols from Wagner et al. (2016), red dot from this study: vicinity of Bamyan town, Bamyan.

Distribution in Afghanistan. According to Wagner et al. (2016), in Afghanistan this species complex comprises four species (B. oblongus, B. pseudoraddei, B. turanensis, B. zugmayeri) that are recorded through the whole of the country except the central Hindu Kush Range (Fig. 17). These toads are known from the provinces of Badakhshan, Badghis, Baglan, Balkh, Bamyan, Farah, Faryab, Ghazni, Helmand, Herat, Kabul, Kandahar, Kunduz, Logar, Nangarhar, Paktia, Samangan, Takhar, Wardak, and Zabul (Wagner et al. 2016 and Fig. 17). One locality presented by Wagner et al. (2016: 463) for B. pseudoraddei, "Culangor [Logar Prov.] (USNM 194595-97)", lacks georeferenced data and is not included on the map. For additional information and unclear localities see remarks (p 462) in Wagner et al. (2016). The specimens noted here confirm a record treated as incertae sedis within the Bufotes viridis complex for Bamyan (Wagner et al. 2016). The record from Bamyan probably belongs to B. baturae (Stöck, Schmid, Steinlein, and Grosse 1999). Whereas Wagner et al. (2016) mentioned this taxon as a subspecies of B. pseudorradei (Mertens, 1971) and Frost et al. (2019) presented both as independent species occurring in Afghanistan (Stöck et al. 2006, Betto-Colliard et al. 2015), we present records of these toads under *B. baturael pseudoraddei* (Fig. 17). The distribution and taxonomy of these toads in Afghanistan needs further research.

Acknowledgments

We would like to thank Vojislav Vasić for collecting the specimens and donating them to the Herpetological Collection of the Institute for the Biological Research "Siniša Stanković", University of Belgrade, Serbia, R Masroor, R Nazarov, VF Orlova, and J Smid for their opinions on the identification of collected specimens and P Wagner for his comments as a reviewer. A special thanks is given to the Editor, AM Bauer, for his help with English and style of the manuscript. The work was supported by the Slovak Research and Development Agency under the contract No. APVV-15-0147 (DJ) and Serbian Ministry of Education, Science and Technological Development, grant no. 173043 (AU, MA, and GD). We dedicate this work to the Afghan people.

References

- Betto-Colliard C, Sermier R, Perrin N, Stöck M (2015) Origin and genome evolution of polyploid green toads in Central Asia: evidence from microsatellite markers. Heredity 114: 300–308. https://doi.org/10.1038/hdy.2014.100
- Böhme W, Szczerbak NN (1991) Ein neuer Wüstenrenner aus dem Hochland Afghanistans, *Eremias (Eremias) afghanistanica* sp. n. (Reptilia: Sauria: Lacertidae). Bonner zoologische Beiträge 42: 137–141.
- Cameron SF, Wynn ML, Wilson RS (2013) Sex-specific trade-offs and compensatory mechanisms: bite force and sprint speed pose conflicting demands on the design of geckos (*Hemidactylus frenatus*). Journal of Experimental Biology 2016: 3781–3789. https://doi. org/10.1242/jeb.083063
- Clark R (1990) A report on herpetological observations in Afghanistan. British Herpetological Society Bulletin 33: 20–42.
- Clark R (1992) Notes on the distribution and ecology of *Phrynocephalus clarkorum* Anderson & Leviton, 1967 and *Phrynocephalus ornatus* Boulenger 1887 in Afghanistan. Herpetological Journal 2: 140–142.
- Džukić G, Tomović L, Andelković M, Urošević A, Nikolić S, Kalezić M (2017) The herpetological collection of the Institute for Biological research "Siniša Stanković", University of Belgrade. Bulletin of the Natural History Museum 10: 57–104. https://doi.org/10.5937/bnhmb1710057d
- Džukić G, Vasić V (1974) Prilog herpetofauni Afganistana (A contribution to the herpetofauna of Afghanistan). IV kongres biologa Jugoslavije, Sarajevo, 25–28 June 1974, Sarajevo.
- Frost DR (2019) Amphibian Species of the World: an Online Reference. Version 6.0. American Museum of Natural History, New York. http://research.amnh.org/herpetology/amphibia/ index.html [February 17, 2019]
- Jablonski D, Lesko AJ (2018) New locality record of the Bengal monitor, *Varanus bengalensis* (Daudin, 1802), from Afghanistan. Herpetology Notes 11: 915–917.
- Kuch U (2004) *Bungarus sindanus*, an addition to the venomous snake fauna of Afghanistan. Herpetozoa 16: 171–173.
- Leviton AE, Anderson SC (1970) The amphibians and reptiles of Afghanistan, A checklist and key to the Herpetofauna. Proceedings of the California Academy of Sciences 38: 163–206.
- Moravec J, Franzen M, Böhme W (2006) Notes on the taxonomy, nomenclature and distribution of the *Trachylepis* (formerly *Mabuya*) *aurata* (Linnaeus, 1758) complex. In: Vences M, Köhler J, Ziegler T, Böhme W (Eds) Herpetologica Bonnensis II. Proceedings of the 13th Congress of the Societas Europaea Herpetologica, 89–93.

- Nahif AA (1986) Bibliographie der zoologischen Literatur über Afghanistan. Bonner Zoologische Beiträge 37: 311–339.
- QGIS Development Team (2018) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org
- Schmidtler JJ, Schmidtler JF (1969) Über *Bufo surdus*; mit einem Schlüssel und Anmerkungen zu den übrigen Kröten Irans und West-Pakistans. Salamandra 5: 113–123.
- Stöck M, Moritz C, Hickerson M, Frynta D, Dujsebayeva TN, Eremchenko VK, Macey JR, Papenfuss TJ, Wake DB (2006) Evolution of mitochondrial relationships and biogeography of Palearctic green toads (*Bufo viridis* subgroup) with insights in their genomic plasticity. Molecular Phylogenetics and Evolution 41: 663–689. https://doi.org/10.1016/j. ympev.2006.05.026
- Vasić FV (1974) Observations ornithologiques en Afghanistan. Alauda 42: 259–280.
- Wagner P, Bauer AM, Leviton AE, Wilms TM, Böhme W (2016) A Checklist of the amphibians and reptiles of Afghanistan, Exploring herpetodiversity using biodiversity archives. Proceedings of the California Academy of Sciences 63: 457–565.

Supplementary material I

Figures S1–S19

Authors: Daniel Jablonski, Aleksandar Urošević, Marko Andjelković, Georg Džukić Data type: Adobe Acrobat Document (.pdf)

- Explanation note: Additional specimens of lizards collected in Afghanistan and their localities in the country from the herpetological collection of the Institute for Bio-logical research "Siniša Stanković", University of Belgrade, Belgrade, Serbia.
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/zookeys.843.29420.suppl1

CHECKLIST



Richness and composition of anuran assemblages from an Amazonian savanna

Carlos Eduardo Costa-Campos^{1,2}, Eliza Maria Xavier Freire^{2,3}

Universidade Federal do Amapá, Departamento de Ciências Biológicas e da Saúde, Laboratório de Herpetologia, Rodovia Juscelino Kubitschek, km 02, Jardim Marco Zero, CEP 68.903-419, Macapá, AP, Brasil
Programa de Pós-Graduação em Psicobiologia, Universidade Federal do Rio Grande do Norte, Centro de Biociências, Lagoa Nova, CEP 59072-970, Natal, RN, Brasil 3 Universidade Federal do Rio Grande do Norte, Departamento de Botânica, Ecologia e Zoologia, Campus Central, Laboratório de Herpetologia, Lagoa Nova, CEP 59072-970, Natal, RN, Brasil

Corresponding author: Carlos Eduardo Costa-Campos (eduardocampos@unifap.br)

Academic editor: A. Cr	rottini	Received 25 January 2019) Accepted 2 March	h 2019	Published 9 May 20
http://zoobank.org/E34BFE1D-3140-456F-A563-E679DEDD60ED					

Citation: Costa-Campos CE, Freire EMX (2019) Richness and composition of anuran assemblages from an Amazonian savanna. ZooKeys 843: 149–169. https://doi.org/10.3897/zookeys.843.33365

Abstract

The Amazonian savannas occupy approximately 150,000 km² of the Brazilian Amazon, occurring in scattered isolated patches over large areas of forest in the states of Amapá, Amazonas, Pará, Roraima and Rondônia. Despite having considerable variation in the Anuran composition between locations and between the savanna's physiognomies, a systematic and geographically wide sampling has not been performed for the savanna from Amapá yet, located in the north of Brazil, eastern Amazonia. In this perspective, a study was conducted on the richness, composition, diversity, and abundance of Anuran species in a savanna area in Amapá State. For Anuran sampling, we performed 24 samples in four physiognomies (grassland savanna, scrub grassland savanna, parkland savanna, open woodland savanna) through an active and auditory search more than 20 sampling plots of 100 × 50 meters in each physiognomy. Twentyone (21) species of frogs belonging to five families were registered: Bufonidae, Hylidae, Leptodactylidae, Microhylidae and Phyllomedusidae. Scrub grassland savanna registered a greater number of individuals regarding the species richness by physiognomy. The species rarefaction curve for the total area reached an asymptote, suggesting that the data collection effort was enough to adequately sample the species richness of the area. The Kruskal-Wallis variance analysis revealed significant differences in the species richness and diversity among the physiognomies. The Bray-Curtis similarity analysis grouped the physiognomies into three main groups: open woodland savanna, grassland savanna and scrub grassland savanna and parkland savanna. Through ordering by non-metric multidimensional scaling, the species composition from the

Copyright C.E. Costa-Campos, E.M.X. Freire. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

savanna anuran assemblage resulted in a separation among three sampled physiognomies with significant differences, indicating differences in assemblage composition of the three sampled physiognomies. The local richness (21 species) corresponds to 14% of the 15 typical species that have strongly associated distribution with the Cerrado from Central Brazil, and 35.6% of 59 typical species of neighboring domains which only marginally occur in the Cerrado, representing a considerable part of frog species richness recorded in the savanna in the eastern portion of the Brazilian Amazon.

Keywords

Amapá, eastern Amazon, frog assemblages, tropical forest, amphibians

Introduction

The Amazonian savannas are usually flat areas covered by open vegetation composed of herbaceous strata dominated by grasses, with trees and shrubs scattered in different coverage densities (Solbrig 1996). They occupy approximately 267,164 km² with almost 90% of the total area occurs in Bolivia and Brazil, occurring in isolated spots spread over large areas of forest in the states of Amapá, Amazonas, Pará, Roraima and Rondônia (Pires and Prance 1985; Sanaiotti et al. 1997) with smaller areas in Venezuela, Guyana and Suriname (Carvalho and Mustin 2017). The largest continuous savanna block are the Beni savannas in Bolivia (127,096 km²); the Guyanan savanna in Brazil, Venezuela and Guyana; the Sipaliwini-Parú savanna in Brazil and Suriname, and the savanna of Amapá in Brazil (13,027 km²) (Pennington et al. 2006, Barbosa et al. 2007, Carvalho and Mustin 2017).

The complexity and heterogeneity found in different savanna phytophysiognomies (Eiten 1972, Coutinho 1978), as well as the influence of neighboring domains, reveal the existence of geographic distribution patterns, diversity, richness and abundance of inhabiting species in these areas (Mesquita et al. 2006). With regard to fauna studies and given the great diversity of anuran amphibians from savannas, the number of studies about assemblage ecology in Amazonian savannas has been increasing over the years, addressing different aspects such as the mechanisms that act on the selection and use of habitats and the factors responsible for maintaining diversity, and in the proper assemblage structures (Menin et al. 2007; Menin et al. 2011; Rojas-Ahumada et al. 2012; Landeiro et al. 2014; Dias-Terceiro et al. 2015; Jorge et al. 2016; Ferrão et al. 2018; Ferreira et al. 2018).

In this context, despite the territorial extension and heterogeneity, the Amazon savannas are extremely unfamiliar areas in terms of their frog communities and are highly threatened by the expansion of human activity, therefore it is urgent to conduct inventories on anuran species (Neckel-Oliveira et al. 2000, Barreto et al. 2007, Bertoluci et al. 2007, Brasileiro et al. 2008, Giaretta et al. 2008, Pinheiro et al. 2012, Lima et al. 2017). The strong anthropic pressure, the high degree of endemism and declining savanna frog populations are other factors that justify the importance of inventories (Stuart et al. 2004, Eterovick et al. 2005).

Despite the considerable variation in the anuran composition between locations and between the Cerrado physiognomies (Neckel-Oliveira et al. 2000, Valdujo et al.

2012), a systematic and geographically wide study has not been performed for the Eastern Amazonia savanna. Therefore, an inventory on the anurans in the savanna area of Amapá was performed in order to know the composition, richness, and diversity along the different physiognomies. In this study, we investigated the following questions: (1) what is the species composition of anurans in the study area? (2) Do the species richness, diversity, and equitability differ between different types of savanna physiognomies? Additionally, we compared our findings with studies conducted in other Amazon savannas and well-sampled areas in the Cerrado in central Brazil.

Materials and methods

Study area

The Amapá savanna occupies a narrow longitudinal band of approximately 140,000 km², which corresponds to 7.2% of the total area of the Amapá State territory (Mustin et al. 2017), is characterised by a mosaic of areas with open woody vegetation, areas with a denser woody shrub layer, and open grassy areas, and by seasonally flooded areas in the transition zone with floodplains (Costa-Neto et al. 2017). In this area, specifically in the Experimental Field of the Brazilian Agricultural Research Corporation – EMBRAPA (00°23'5"N; 51°02'2"W), the present study was conducted in a total area of 1,381 hectares and a perimeter of 15,080 m (Figure 1).

Four savanna physiognomies were sampled (cf. Miranda et al. 2003; Melém-Júnior et al. 2003): (1) grassland savanna (GS), characterized by extensive grass fields, abundant herbaceous stratus and woody stratus well dispersed by the continuous herbaceous stratus and sparse dwarf trees (< 1.0 m high); (2) scrub grassland savanna (SG), with herbaceous stratus covered by grass with a large density and tree stratus with irregular presence and sparse small trees (< 3.8 m high); (3) parkland savanna (PS), with less developed herbaceous stratus and thicker arboreal tree cover (< 4.3 m high) forming a discontinuous canopy; and (4) open woodland savanna (OW), with and absent of herbaceous stratus with higher density, forming a closed canopy (> 2.0 m high).

The predominant climate type is Ami (tropical rainy climate with short dry period) according Köppen-Geiger classification. Due to the concentration of rainfall in six consecutive months (January – July), the climate throughout the year can be typically recognized in only two seasons: a quite clear dry season and a rainy season with high rainfall. Regarding the monthly average temperature, the minimum is 24.4 °C and maximum 28.4 °C (Alvares et al. 2013). Summarized data is displayed in Figure 2.

The terrain is flat or gently hilly on soils that occur in two main forms, being oxisols and quartz sands. The savanna domain occurs on two basic types of terrain: crystalline or sedimentary plateaus and interplateau depressions. In general, the regions of plateaus predominate in the interfluvia wider savanna forms, while the interplateau depressions occur in denser cerrado (Aguiar et al. 2004).



Figure 1. Maps showing the Amapá state and sampling sites in the Experimental Field of the Brazilian Agricultural Research Corporation – EMBRAPA, municipality of Macapá, Amapá State, northern Brazil.



Figure 2. Rainfall data and minimum and maximum temperatures at the Experimental Field of the Brazilian Agricultural Research Corporation – EMBRAPA, municipality of Macapá, Amapá State, northern Brazil between January and December 2009, 2010, and 2013.

Sampling design

For the anuran sampling plot 24 incursions into each physiognomy were conducted, 12 in the rainy season and 12 in the dry season. Twenty (20) sampling units were established in each physiognomy (grassland savanna, scrub grassland savanna, parkland savanna and open woodland savanna), arranged according to the availability of water bodies. Each sample unit was represented by a portion of 100×50 meters (0.5 ha), at least 500 meters away from each other. Active and auditory visual searches were conducted in these sampling units (Crump and Scott 1994, Heyer et al. 1994, Zimmerman 1994). The sampling effort was the same in the four physiognomies to enable comparisons. The species taxonomy applied follows the Brazilian Society of Herpetology (SBH), according to Segalla et al. (2016) and Dubois (2017).

The active visual and auditory search was performed in each sampling plot by four researchers from 18:00 to 00:00. The number of individuals of each species calling activity was recorded every 10 minutes. The sampling effort was calculated by multiplying the number of hours in the field by the number of researchers involved in the collection in both methods, resulting in a sampling effort of 1,920 hours/man. All collected specimens were anesthetized and killed, fixed in 10% formaldehyde and stored in 70% ethanol. Voucher specimens are deposited at the Herpetological Collection of the Universidade Federal do Amapá (UNIFAP), under the care of Carlos Eduardo Costa Campos (CECCAMPOS) (Appendix 1).

Data analysis

The amphibian species diversity of between the four studied savanna physiognomies was calculated through the Shannon-Wiener diversity Index (Krebs 1999), where H' = species diversity index, pi = Ni / N = probability that an individual belongs to species *i* in total "*S*" species, Ni = total number of individuals of the species *i*, N = total number of species.

$$H' = \sum (pi)l = 1 (\ln pi)$$

The equitability index was calculated by the ratio between the diversity obtained and the maximum diversity, where j = equitability, H' = achieved diversity. *Hmax'* = maximum diversity. This index shows the population homogeneity or how the species are represented by the number of individuals of each species in the assemblage (Magurran 2004). This index ranges from 0, when a species excels in abundance, to 1, when species are equally abundant in the environment.

$$J = \frac{H'}{Hmax'}$$

To analyze the anuran species richness, accumulation curves of species were built based on the number of individuals and number of samples (Gotelli and Colwell 2001, 2011) using the EstimateS 9.1 program (Colwell 2013) with 1,000 randomizations. Considering the diverse richness estimators available, we chose to use the Jackknife algorithm first order based on its performance when compared to other estimators (Magurran 2004; Hortal et al. 2006; Reese et al. 2014)

The possible differences in the richness variations, diversity, and equitability in the different physiognomies were verified through one-way ANOVA, Kruskal-Wallis and Dunn tests a posteriori (Zar 2010). All the analyses were performed through the BioEstat 5.0 (Ayres et al. 2007) and PAST 2.09 (Hammer et al. 2001) programs. The values were considered significant at p < 0.05.

To verify if the assemblage composition differs between physiognomies, a cluster analysis (Cluster Analysis) and spatial Non-Metric Multidimensional Scaling (NMDS) were performed. The differences between the species composition and physiognomies were evaluated using an Analysis of Similarity ANOSIM (Clarke 1993). A percentage break analysis of the Similarity (SIMPER) considering the Bray-Curtis similarity index was used to detect which frog species are responsible for the differences between the groups.

Results

Species composition

We recorded 21 anuran species belonging to the following families were obtained: Bufonidae (3 species), Hylidae (10 species), Leptodactylidae (6 species); Microhylidae (1 species), and Phyllomedusidae (1 species) (Table 1, Figure 3). From the recorded species in the study area, three representatives of the Hylidae, Leptodactylidae and Microhylidae families (*Scinax fuscomarginatus, Pseudopaludicola boliviana, Elachistocleis helianneae*, respectively) were recently reported for the first time in the Amapa state by these three studies (Costa-Campos and Freire 2014, Costa-Campos and Freire 2015, Costa-Campos et al. 2016).

Sample efficiency: species rarefaction curve and richness estimators

A slight tendency toward stabilization can be observed in the species accumulation curve (Figure 4), suggesting that the data collection effort was enough to adequately sample the species richness of the studied area. The estimated richness for the study area provided by the richness estimators was 21 species.

Species diversity and equitability

The species diversity obtained the sampled physiognomies ranged from $H \doteq 0.814$ to H' = 2.728, and the equitability ranged from 0.587 to 1.887. The highest diversity of

Table 1. List of anuran species registered at the savanna area in Amapá state, municipality of Macapá. Gray blocking denotes anurans sampled in each physiognomies. Sampled physiognomies: **GS** grassland savanna; **SG** scrub grassland savanna; **PS** parkland savanna; **OW** open woodland savanna. **N** number of individuals recorded. Number of species per family in parentheses.

Family/Species	Sampled physiognomies				Ν
	GS	SG	PS	OW	
Bufonidae (3)					
Rhinella major (Muller & Helmich, 1936)					10
Rhinella marina (Linnaeus, 1758)					5
<i>Rhinella</i> sp.					14
Hylidae (10)					
Boana multifasciata (Günther, 1859)					20
Boana punctata (Schneider, 1799)					18
Boana raniceps Cope, 1862					15
Dendropsophus cf. walfordi (Bokermann, 1962)					8
Osteocephalus taurinus Steindachner, 1862					10
Scinax fuscomarginatus (A. Lutz, 1925)					1
Scinax nebulosus (Spix, 1824)					32
Scinax ruber (Laurenti, 1768)					18
Scinax x-signatus (Spix, 1824)					12
Trachycephalus typhonius (Linnaeus, 1758)					27
Leptodactylidae (Leiuperinae) (1)					
Pseudopaludicola boliviana Parker, 1927					14
Leptodactylidae (Leptodactylinae) (5)					
Adenomera hylaedactyla (Cope, 1868)					32
Leptodactylus fuscus (Schneider, 1799)					30
Leptodactylus macrosternum Miranda-Ribeiro, 1926					5
Leptodactylus pentadactylus (Laurenti, 1768)					8
Leptodactylus podicipinus (Cope, 1862)					12
Microhylidae (Gastrophryninae) (1)					
Elachistocleis helianneae Caramaschi, 2010					14
Phyllomedusidae (1)					
Pithecopus hypochondrialis (Daudin, 1800)					17

Table 2. Kruskal-Wallis variance analysis and the Dunn test performed later between the species richness, diversity and equitability between the savanna physiognomies in Amapá. The significant results are in bold (p < 0.05).

Physiognomies	Richness	H'	J
Grassland savanna and scrub grassland savanna	4.318	4.044	2.173
Grassland savanna and parkland savanna	0.093	0.331	0.150
Grassland savanna and open woodland savanna	1.479	1.619	1.795
Scrub grassland savanna and parkland savanna	4.412	4.375	2.323
Scrub grassland savanna and open woodland savanna	5.798	5.663	3.969
Parkland savanna and open woodland savanna	1.386	1.287	1.645

species was recorded at scrub grassland savanna ($H \doteq 2.459$; N = 19 species), followed by grassland savanna ($H \doteq 2.276$; N = 13 species). The Kruskal-Wallis variance analysis revealed significant differences between the species richness, diversity, dominance (1-D) and equitability between the sampled physiognomies (p < 0.0001). The Dunn test results performed later showed significant differences in species richness, diversity and equitability between the Amapá savanna physiognomies (Table 2).



Figure 3. Anurans recorded in the savanna area from the Experimental Field of the Brazilian Agricultural Research Corporation – EMBRAPA, municipality of Macapá, Amapá State, northern Brazil: **A** *Rhinella major* **B** *Rhinella* sp. **C** *R. marina* **D** *Boana multifasciata* **E** *B. punctata* **F** *B. raniceps* **G** *Dendropsophus* cf. *walfordi* **H** *Osteocephalus taurinus* **I** *Scinax fuscomarginatus* **J** *S. nebulosus.*



Figure 3. Continued: **K** S. ruber **L** S. x-signatus **M** Trachycephalus typhonius **N** Pseudopaludicola boliviana **O** Adenomera hylaedactyla **P** Leptodactylus fuscus **Q** L. macrosternum **R** L. pentadactylus **S** L. podicipinus **T** Pithecopus hypochondrialis, and **U** Elachistocleis helianneae.



Figure 4. The species accumulation curves sampled in the savanna area from the Experimental Field of the Brazilian Agricultural Research Corporation – EMBRAPA, municipality of Macapá, Amapá State, northern Brazil, for each of the sampled physiognomies: **A** grassland savanna **B** scrub grassland savanna **C** parkland savanna **D** open woodland savanna, based on the number of individuals representing the observed (Sobs) and estimated species richness (Jackknife 1).

Similarity and non-metric Multidimensional Scaling (MDS) between different physiognomies from the studied savanna

The similarity analysis from the Bray-Curtis index separated the physiognomies into three main groups: (A) open woodland savanna, (B) grassland savanna and scrub grassland savanna (C) parkland savanna. The group (A) is characterized by the higher *Rh*-*inella* sp. occurrence frequency. For the group (B), the most frequent species were *P. hypochondrialis* and *L. fuscus*. In addition, the last group (C) is characterized by the high frequency of occurrence of *B. punctata* (Figure 5).

The similarity analysis (SIMPER) evaluated the contribution of each species and showed that the average similarity within physiognomies was 27.48 for the grassland savanna, 48.84 for scrub grassland savanna, 58.70 open woodland savanna and 47.02 for parkland savanna. For the grassland savanna, the *L. fuscus* species contributed the most to the average similarity with 53.64, followed by *B. multifasciata* (13.94) and *T. typhonius* (13.64). For scrub grassland savanna, the *P. hypochondrialis* species contributed the most to the average similarity with 26.68 of contribution, followed by *L. fuscus* (18.43) and *S. nebulosus* (16.25). For the open woodland savanna, the *Rhinella* sp. (88.40) and *A. hylaedactyla* species (11.27) were those that contributed the most



Figure 5. Dendrogram of similarity between the savanna area physiognomies, sampled in the Experimental Field of the Brazilian Agricultural Research Corporation – EMBRAPA, municipality of Macapá, Amapá State. Group A (open woodland savanna, OW), Group B (Parkland savanna, PS), and Group C (grassland savanna, GS and scrub grassland savanna, SG).

to the average similarity. For the parkland savanna, *B. punctata* (81.84) and *B. raniceps* species (8.44) contributed the most to the average similarity.

The assemblage average dissimilarity between physiognomies was larger between: open woodland savanna and parkland savanna (99.53); the scrub grassland savanna and the open woodland savanna (97.48); the grassland savanna and the open woodland savanna (96.45); the grassland savanna and the parkland savanna (96.22); the scrub grassland savanna and the parkland savanna (94.85); and lower between grassland savanna and scrub grassland savanna (75.18). Regarding the total differences, the species that contributed most to the average dissimilarity between areas were: *Rhinella* sp. (open woodland savanna and parkland savanna, 32.0%); *B. punctata* (grassland savanna and scrub grassland savanna, 21.7%); and *P. hypochondrialis* (grassland savanna and scrub grassland savanna, 17.37%).

Through the MDS constructed from the Bray-Curtis similarity matrix, it has been shown that the anuran assemblage in the study area is distributed between three sampled physiognomies, formed by 1) grassland savanna and scrub grassland savanna, 2) parkland savanna, and 3) open woodland savanna, with significant differences (ANO-SIM, R = 0.823, p <0.001) and stress level of 0.07. In this way, the assemblage formed distinct groups in the MDS, indicating differences in the assemblage species composition of the four physiognomies (Figure 6).



Figure 6. Order by MDS of physiognomies in the savanna area physiognomies, sampled in the Experimental Field of the Brazilian Agricultural Research Corporation – EMBRAPA, municipality of Macapá, Amapá State generated from the Bray-Curtis similarity matrix. Grassland savanna (GS); scrub grassland savanna (SG); parkland savanna (PS); open woodland savanna (OW).

Discussion

The registered richness supports the estimated richness of 18-43 species in well sampled locations in the Cerrado of Central Brazil (Brasileiro et al. 2005, Vasconcelos and Rossa-Feres 2005, Santos et al. 2007, Brasileiro et al. 2008, Ribeiro-Jr and Bertoluci 2009, Araújo and Almeida-Santos 2011) and in Amazonian savannas (Neckel-Oliveira et al. 2000, Pinheiro et al. 2012, Bitar et al. 2012, Neckel-Oliveira et al. 2012, Lima et al. 2017). The local richness corresponds to 14% of the 150 species which have distribution strongly associated with the Cerrado, and 35.6% of the 59 typical species of neighboring domains and which only marginally occur in the Cerrado (Valdujo et al. 2011, 2012), representing 21 anuran species recorded in the savannas of the eastern portion of the Brazilian Amazon.

The anuran species richness of the studied savanna varied in different physiognomies, where the open formations (e.g., grassland savanna) had greater richness, followed by forest formations (e.g., parkland and open woodland savanna). This is probably a reflex of the proportion of abundant and rare species in each physiognomy (Magurran 2004). These data agree with other studies, which suggest that the open formations tend to have higher richness when compared to forest formations of the Domain Cerrado (Maffei et al. 2011). Studies carried out by Strüssmann et al. (2000), Brandão and Araújo (2002) and Valdujo et al. (2011) found higher anuran richness in open savanna formations than in the gallery forest. This is due to the fact that the reproduction of most savanna species occurs in open areas, and as the availability of breeding sites is one of the most important factors in the selection of habitat for anurans, higher species richness and abundance of individuals is expected in open physiognomies (Colli et al. 2002, Bastazini et al. 2007).

On the other hand, in the study performed by Neckel-Oliveira et al. (2000) in an area of the Amazonian savanna in the municipality of Santarém, by Pinheiro et al. (2012) in the Carajás region, both in the state of Pará, and by Lima et al. (2017) in the Amazonian Savanna of the Rio Curiaú Environmental Protection Area in Amapá, higher richness and abundance of anuran species were found in forested environments. Several studies report that species of open environments can use forested areas as sites for foraging, migration, reproduction, or refuge (Brassaloti et al. 2010, Oda et al. 2016, Santos and Conte 2016).

Furthermore, several studies have shown that complex and heterogeneous environments facilitate the coexistence of more species when compared to homogeneous environments (Conte and Rossa-Feres 2007, Santos et al. 2007, Vasconcelos et al. 2009, Silva et al. 2011). In addition to the heterogeneity and biodiverse of the Cerrado (Silva et al. 2006), differences in their composition and species richness between various sampled locations must have been favored by the contact with four major phytogeographic domains from South America: Amazonia, Atlantic Forest, Caatinga, and Chaco (Joly et al. 1999).

Despite the species cumulative curve having a tendency to stabilize, the possibility of local richness expansion is not unlikely, but as the study continues, an increased effort would contribute very slowly to adding to the species richness, as evidenced by richness estimators. This highlights the importance of accomplishing inventories with the association of different sampling methods for a more complete knowledge of anurans (Greenberg et al. 1994, Brown 1997, Maritz et al. 2007; Ribeiro-Jr et al. 2008), as the species richness is closely related to the sampling effort.

According to Santos (2006), accumulation curves are excellent for evaluating the inventories efficiency in the record of all species of certain sites or habitats. Similar to the rarefaction for the total area, the species accumulation curves for all physiognomies also stabilized; however, for the tree savanna stabilized in a relatively low species richness, this indicates that the additional sample effort would be necessary in the forest environments. In this context, three non-mutually exclusive factors and associated to the canopy cover structure may be responsible for the different richness patterns and frog species composition observed in the studied physiognomies: 1) some species ability in colonizing environments characterized by sparser vegetation; 2) the species distinct physiological tolerances concerning water temperature, light intensity and humidity near the soil surface; and 3) specific microenvironment dependence on specific sites for breeding.

In terms of diversity by physiognomies, the greatest diversity was found in scrub grassland savanna. The higher diversity recorded in the scrub grassland savanna corroborates comparative studies of the species diversity of open formations with grasslands backgrounds, savanna and forest in the Cerrado (Brasileiro et al. 2005, Araújo et al. 2009, Araújo and Almeida-Santos 2011, Valdujo et al. 2011). The diversity and equitability rates showed significant differences between sampled physiognomies. This result was expected due to the differences present in the physiognomies in the environmental heterogeneity (Vasconcelos et al. 2009, 2010), as this heterogeneity has an important role in determining species richness and in the assemblage structure by providing environments and several conditions for species with different ecophysiological requirements (Huston 1994, Buckley and Jetz 2007).

The obtained Bray-Curtis index seems coherent, presenting groupings that reflect differences between the main sampled physiognomies and revealing greater similarity between the grassland savanna and the scrub grassland savanna. Both physiognomies differ in the floristic composition of the dominant tree species, shrub and herbaceous substrate, and topography (Batalha 2011), and these differences have probably influenced the obtained results. However, geographically close areas generally exhibit similar structural features, which support similar assemblages in their richness and diversity (Dixo and Verdade 2006). Even though they do not favor species with more limited needs, the parkland savanna and open woodland savanna physiognomies, with lower structural complexity, are relatively favorable for structuring frog assemblages, thus potentially contributing to the preservation of regional diversity in mosaic vegetation areas (Gardner et al. 2006).

The Amapá savanna although scarcely known, may suffer from the agricultural expansion of grain production, extensive cattle ranching and urban growth, leading to habitat loss and vegetation fragmentation. Coupled with the wide diversity of anurans found in the area and the finding of new species and new records for Amapá State make Amapá savanna a hotpoint for anurans within the Amazon Forest hotspot (Silva and Bates 2002; Lima et al. 2017, Mustin et al. 2017) and, consequently, a place for the implementation of priority conservation measures aiming the increase of the protected area.

Acknowledgements

We are grateful to the Brazilian Agricultural Research Corporation – EMBRAPA/ Amapá (Experimental Field) for allowing us access to research areas under their care and for logistical assistance. We thank the Fundação de Amparo à Pesquisa do Estado do Amapá/FAPEAP (process 250.203/059/2014). We thank Ananda Araújo and Telma Lobato for assistance in the field. We thank two anonymous reviewers for valuable suggestions that greatly improved this paper; and we are grateful the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) for providing collection permits (SISBIO/18243-1).

References

- Aguiar LMS, Machado RB, Marinho-Filho J (2004) A diversidade biológica do Cerrado. In: Aguiar LM, Camargo AJA (Eds) Cerrado: ecologia e caracterização. Embrapa Cerrados, Brasília, 17–40.
- Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22(6): 711–728. https://doi. org/10.1127/0941-2948/2013/0507
- Araújo CO, Almeida-Santos SM (2011) Herpetofauna de um remanescente de cerrado no estado de São Paulo, sudeste do Brasil. Biota Neotropica 11(3): 47–62. https://doi. org/10.1590/S1676-06032011000300003
- Araújo CO, Condez TH, Sawaya RJ (2009) Anfíbios Anuros do Parque Estadual das Furnas do Bom Jesus, sudeste do Brasil, e suas relações com outras taxocenoses no Brasil. Biota Neotropica 9(2): 77–98. https://doi.org/10.1590/S1676-06032009000200007
- Ayres M, Ayres Jr MA, Ayres DL, Dos Santos AS (2007) BioEstat: aplicações estatísticas nas áreas das ciências biológicas e médicas. Publicações Avulsas Mamirauá, Belém, 364 pp.
- Barbosa RI, Campos C, Pinto F, Fearnside PM (2007) The "Lavrados" of Roraima: Biodiversity and Conservation of Brazil's Amazonian Savannas. Functional Ecosystems and Communities 1: 29–41.
- Barreto L, Arzabe C, Lima YCC (2007) Herpetofauna da região de Balsas. In: Barreto L (Ed.) Cerrado Norte do Brasil. União Sul-Americana de Estudos da Biodiversidade, Pelotas, 213–219.
- Bastazini CV, Munduruca JV, Rocha PLB, Napoli MF (2007) Which environmental variables better explain changes in anuran community composition? A case study in the Restinga of Mata de São João, Bahia, Brazil. Herpetologica 63: 459–471. https://doi.org/10.1655/0018-0831(2007)63[459:WEVBEC]2.0.CO;2
- Batalha MA (2011) O Cerrado não é um bioma. Biota Neotropica 11(1): 21–24. https://doi. org/10.1590/S1676-06032011000100001
- Bertoluci J, Brassaloti RA, Ribeiro-Jr JW, Vilela VMFN, Sawakuchi HO (2007) Species composition and similarities among anuran assemblages of forest sites in southeastern Brazil. Scientia Agricola 64(4): 364–374. https://doi.org/10.1590/S0103-90162007000400007
- Bitar YOC, Pinheiro LPC, Abe PS, Santos-Costa MC (2012) Species composition and reproductive modes of anurans from a transitional Amazonian forest, Brazil. Zoologia 29(1): 19–26. https://doi.org/10.1590/S1984-46702012000100003
- Brandão RA, Araújo AFB (2002) A herpetofauna associada a matas de galeria no Distrito Federal. In: Ribeiro JF, Fonseca CEL, Sousa-Silva JC (Eds) Cerrado: caracterização e recuperação de matas de galeria. EMBRAPA Cerrados, Brasília, 560–604.
- Brasileiro CA, Sawaya RJ, Kiefer MC, Martins M (2005) Amphibians of an open cerrado fragment in southeastern Brazil. Biota Neotropica 5(2): 93–109. https://doi.org/10.1590/ S1676-06032005000300006
- Brasileiro CA, Lucas LM, Oyamaguchi HM, Thomé MTC, Dixo M (2008) Anurans, Northern Tocantins River Basin, states of Tocantins and Maranhão, Brazil. Check List 4(2): 185–197. https://doi.org/10.15560/4.2.185

- Brassaloti RA, Rossa-Feres DC, Bertoluci J (2010) Anurofauna da floresta estacional semidecidual da Estação Ecológica dos Caetetus, sudeste do Brasil. Biota Neotropica 10(1): 275– 291. https://doi.org/10.1590/S1676-06032010000100024
- Brown LJ (1997) An evaluation of some marking and trapping techniques currently used in the study of anuran population dynamics. Journal of Herpetology 31: 410–419. https://doi. org/10.2307/1565670
- Buckley L, Jetz BW (2007) Environmental and historical constraints on global patterns of amphibian richness. Proceedings of the Royal Society 274: 1167–1173. https://doi. org/10.1098/rspb.2006.0436
- Carvalho WD de, Mustin K (2017) The highly threatened and little known Amazonian savannahs. Nature Ecology & Evolution 1: 100. https://doi.org/10.1038/s41559-017-0100
- Clarke KR (1993) Non-parametric multivariate analysis of changes in community structure. Austral Ecology 18: 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x
- Costa-Campos CE, Freire EMX (2014) Geographic Distribution. *Scinax trilineatus*. Brazil: Amapá: Municipality of Macapá. Herpetological Review 45(3): 459.
- Costa-Campos CE, Freire EMX (2015) Distribution extension and geographic distribution map of *Elachistocleis helianneae* (Anura: Microhylidae): new record for state of Amapá, Eastern Amazon. Check List 11(5): 1747. https://doi.org/10.15560/11.5.1747
- Costa-Campos CE, Carvalho TR, Freire EMX (2016) First record of *Pseudopaludicola boliviana* Parker, 1927 (Anura, Leptodactylidae, Leiuperinae) in the Brazilian state of Amapá, with comments on its advertisement call and distribution. Check List 12(6): 1991. https://doi. org/10.15560/12.6.1991
- Costa-Neto SV, Miranda I, Rocha AES (2017) Flora das savanas do estado do Amapá. In: Bastos A, Miranda-Júnior J, Silva R (Eds) Conhecimento e manejo sustentável da biodiversidade amapaense. Blucher, São Paulo, 65–94. https://doi.org/10.5151/9788580392197-04
- Colli GR, Bastos RP, Araújo AFB (2002) The character e dynamics of the Cerrado Herpetofauna. In: Oliveira PS, Marquis RJ (Eds) The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, Nova York, 223–241. https:// doi.org/10.7312/oliv12042-013
- Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9.1. http://purl.oclc.org/estimates [Accessed on 15 July 2017]
- Conte CE, Rossa-Feres DC (2007) Riqueza e distribuição espaço-temporal de anuros em um remanescente de Floresta de Araucária no sudeste do Paraná. Revista Brasileira de Zoologia 24(4): 1025–1037. https://doi.org/10.1590/S0101-81752007000400020
- Coutinho LM (1978) O conceito de cerrado. Revista Brasileira de Botânica 1: 17-23.
- Crump ML, Scott NJJ (1994) Visual encounter surveys. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LAC, Foster MS (Eds) Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington, 84–92.
- Dias-Terceiro RG, Kaefer IL, Fraga R, Araújo MC, Simões PI, Lima AP (2015) A matter of scale: historical and environmental factors structure anuran assemblages from the Upper Madeira River, Amazonia. Biotropica 47(2): 259–266. https://doi.org/10.1111/btp.12197
- Dixo M, Verdade VK (2006) Herpetofauna de serrapilheira da Reserva Biológica de Morro Grande, Cotia (SP). Biota Neotropica 6(2): 1–20. https://doi.org/10.1590/S1676-06032006000200009

- Dubois A (2017) The nomenclatural status of *Hysaplesia*, *Hylaplesia*, *Dendrobates* and related nomina (Amphibia, Anura), with general comments on zoological nomenclature and its governance, as well as on taxonomic databases and websites. Bionomina 11: 1–48. https://doi.org/10.11646/bionomina.11.1.1
- Eiten G (1972) The Cerrado vegetation of Brazil. The Botanical Review 38: 201-341.
- Eterovick PC, Carnaval ACOQ, Borges-Nojosa DM, Silvano DL, Segalla MV, Sazima I (2005) Amphibian declines in Brazil: an overview. Biotropica 37(2): 166–179. https://doi. org/10.1111/j.1744-7429.2005.00024.x
- Ferrão M, de Fraga R, Moravec J, Kaefer IL, Lima AP (2018) A new species of Amazonian snouted treefrog (Hylidae: *Scinax*) with description of a novel species-habitat association for an aquatic breeding frog. PeerJ 6: e4321. https://doi.org/10.7717/peerj.4321
- Ferreira AS, Jehle R, Stow AJ, Lima AP (2018) Soil and forest structure predicts large-scale patterns of occurrence and local abundance of a widespread Amazonian frog. PeerJ 6: e5424. https://doi.org/10.7717/peerj.5424
- Gardner TA, Ribeiro-Jr. MA, Barlow J, Ávila-Pires TCS, Hoogmoed MS, Peres CA (2006) The Value of Primary, Secundary, and Plantation Forest for a Neotropical Herpetofauna. Conservation Biology 21(3): 775–787. https://doi.org/10.1111/j.1523-1739.2007.00659.x
- Giaretta AA, Menin M, Facure KG, Kokubum MN, Oliveira Filho JC (2008) Species richness, relative abundance, and habitat of reproduction of terrestrial frogs in the Triângulo Mineiro region, Cerrado biome, southeastern Brazil. Iheringia, Série Zoologia 98(2): 181–188. https://doi.org/10.1590/S0073-47212008000200002
- Gotelli N, Colwell RK (2001) Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379–391. https://doi. org/10.1046/j.1461-0248.2001.00230.x
- Gotelli NJ, Colwell RK (2011) Estimating species richness. In: Magurran AE, McGill BJ (Eds) Frontiers in Measuring Biodiversity. Oxford University Press, New York, 39–54.
- Greenberg CH, Neary DG, Harris LD (1994) A comparison of herpetofaunal sampling effectiveness of pitfall, single-ended, and double-ended funnel traps with drift fences. Journal of Herpetology 28: 319–324. https://doi.org/10.2307/1564530
- Hammer O, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics software package for education and data analysis. Version 2.01. http://palaeo-electronica.org/2001_1/past/ issue1_01.htm [Accessed on 15 August 2017]
- Heyer WR, Donnelly MA, McDiarmid RW, Hayek LAC, Foster MS (1994) Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington, 364 pp.
- Hortal J, Borges PAV, Gaspare C (2006) Evaluating the performance of species richness estimators: sensitivity to sample grain size. Journal of Animal Ecology 75: 274–287. https://doi. org/10.1111/j.1365-2656.2006.01048.x
- Huston MA (1994) Biological Diversity. The coexistence of species changing landscape. Cambridge University Press, UK, 681 pp.
- Joly CA, Aidar MPM, Klink CA, Mcgrath DG, Moreira AG, Moutinho P, Nepstad DC, Oliveira AA, Pott A, Rodal MJN, Sampaio EVSB (1999) Evolution of the Brazilian phytogeography classification systems: implications for biodiversity conservation. Ciência e Cultura 51: 331–348.

- Jorge RF, Simões PI, Magnusson WE, Lima AP (2016) Fine-scale habitat heterogeneity explains the local distribution of two Amazonian frog species of concern for conservation. Biotropica 48(5): 697–703. https://doi.org/10.1111/btp.12333
- Krebs CJ (1999) Ecological methodology. 2° Edition. Benjamin/Cummings, Menlo Park, California, 620 pp.
- Landeiro VL, Waldez F, Menin M (2014) Spatial and environmental patterns of Amazonian anurans: Differences between assemblages with aquatic and terrestrial reproduction, and implications for conservation management. Natureza & Conservação 12(1): 42–46. https://doi.org/10.4322/natcon.2014.008
- Lima JRF, Lima JD, Lima SD, Lima-Silva RB, Andrade GV (2017) Amphibians found in the Amazonian Savanna of the Rio Curiaú Environmental Protection Area in Amapá, Brazil. Biota Neotropica 17(2): e20160252. https://doi.org/10.1590/1676-0611-bn-2016-0252
- Maffei F, Ubaid FK, Jim J (2011) Anurans in an open cerrado area in the municipality of Borebi, Sao Paulo state, Southeastern Brazil: habitat use, abundance and seasonal variation. Biota Neotropica 11: 221–233. https://doi.org/10.1590/S1676-06032011000200023
- Magurran AE (2004) Measuring biological diversity. Blackwell Science, Oxford, 256 pp.
- Maritz B, Gavin M, Mackay D, Alexander G (2007) The effect of funnel trap type and size of pitfall trap on trap success: implications for ecological field studies. Amphibia-Reptilia 28: 321–328. https://doi.org/10.1163/156853807781374746
- Melém-Júnior NJ, Farias-Neto JT, Yokomizo GKI (2003) Caracterização dos Cerrados do Amapá. Comunicado Técnico Embrapa 105: 1–5.
- Menin M, Lima AP, Magnusson WE, Waldez F (2007) Topographic and edaphic effects on the distribution of terrestrially reproducing anurans in Central Amazonia: mesoscale spatial patterns. Journal of Tropical Ecology 23: 539–547. https://doi.org/10.1017/S0266467407004269
- Menin M, Waldez F, Lima AP (2011) Effects of environmental and spatial factors on the distribution of anuran species with aquatic reproduction in central Amazonia. Herpetological Journal 21: 255–261.
- Mesquita DO, Colli GR, França FGR, Vitt LJ (2006) Ecology of a Cerrado lizard assemblage in the Jalapão Region of Brazil. Copeia 2006: 460–471. https://doi.org/10.1643/0045-8511(2006)2006[460:EOACLA]2.0.CO;2
- Miranda IS, Absy ML, Rebêlo GH (2003) Community Structure of Woody Plants of Roraima Savannahs, Brazil. Plant Ecology 164: 109–123. https://doi.org/10.1023/A:1021298328048
- Mustin K, Carvalho WD, Hilário RR, Costa-Neto SV, Silva CR, Vasconcelos IM, Castro IJ, Eilers V, Kauano ÉE, Mende-Júnior, RNG, Funi C, Fearnside PM, Silva, JMC, Euler AMC, Toledo, JJ (2017) Biodiversity, threats and conservation challenges in the Cerrado of Amapá, an Amazonian savanna. Nature Conservation 22: 107–127. https://doi. org/10.3897/natureconservation.22.1382
- Neckel-Oliveira S, Magnusson WE, Lima, AP (2000) Diversity and distribution of frogs in an Amazonian savanna in Brazil. Amphibia-Reptilia 21(3): 317–326. https://doi. org/10.1163/156853800507516
- Neckel-Oliveira S, Galatti U, Gordo M, Pinheiro LPC, Maschio GF (2012) Anfíbios. In: Martins FD, Castilho AF, Campos J, Hatano FM, Rolim SG (Eds) Fauna da Floresta Nacional de Carajás: Estudos Sobre Vertebrados Terrestres. Editora Rona, São Paulo, 67–79.

- Oda FH, Batista VG, Gambale PG, Mise FT, Souza F, Bellay S, Ortega JCG, Takemoto RM (2016) Anuran Species Richness, Composition, and Breeding Habitat Preferences: a Comparison between Forest Remnants and Agricultural Landscapes in Southern Brazil. Zoological Studies 55: 34. https://doi.org/10.6620/ZS.2016.55-34
- Pennington RT, Lewis GP, Ratter JA (2006) An overview of the plant diversity, biogeography and conservation of Neotropical savannas and seasonally dry forests. In: Pennington RT, Lewis GP, Ratter JA (Eds) Neotropical savannas and dry forests: plant diversity, biogeography, and conservation. Taylor & Francis CRC Press, Oxford, 1–29. https://doi. org/10.1201/9781420004496.ch1
- Pinheiro LC, Bitar YOC, Galatti U, Neckel-Oliveira S, Santos-Costa MC (2012) Amphibians from southeastern state of Pará: Carajás Region, northern Brazil. Check List 8(4): 693–702. https://doi.org/10.15560/8.4.693
- Pires JM, Prance GT (1985) The vegetation types of the Brazilian Amazon. In: Prance GT, Lovejoy TE (Eds) Amazonia. Pergamon Press, Oxford, 109–145.
- Reese GC, Wilson KR, Flather CH (2014) Performance of species richness estimators across assemblage types and survey parameters. Global Ecology and Biogeography 23: 585–594. https://doi.org/10.1111/geb.12144
- Ribeiro-Jr JW, Bertoluci J (2009) Anurans of the cerrado of the Estação Ecológica and the Floresta Estadual de Assis, southeastern Brazil. Biota Neotropica 9(1): 207–206. https://doi. org/10.1590/S1676-06032009000100020
- Ribeiro-Jr MA, Gardner TA, Ávila-Pires TCS (2008) Evaluating the effectiveness of herpetofaunal sampling techniques across a gradient of habitat change in a tropical forest landscape. Journal of Herpetology 42(4): 733–749. https://doi.org/10.1670/07-097R3.1
- Rojas-Ahumada DP, Landeiro VL, Menin M (2012) Role of environmental and spatial processes in structuring anuran communities across a tropical rain forest. Austral Ecology 37: 865–873. https://doi.org/10.1111/j.1442-9993.2011.02330.x
- Sanaiotti T, Bridgewater S, Ratter J (1997) A floristic study of the savanna vegetation of the state of Amapá, Brazil, and suggestions for its conservation. Boletim do Museu Paraense Emílio Goeldi, Série Botânica 13: 3–29.
- Santos AJ (2006) Estimativas de riqueza em espécies. In: Cullen Júnior L, Rudran R, Valladares-Pádua C (Eds) Métodos de estudos em biologia da conservação e manejo da vida silvestre. Editora UFPR, Curitiba, 19–41.
- Santos P, Siqueira CC, Goyannes-Araújo P, Fernandes CGA, Rubião ECN, Van Sluys M (2007) A Survey of the Leaf-Litter Frog Assembly from an Atlantic Forest Area (Reserva Ecológica de Guapiaçu) in Rio de Janeiro State, Brazil, with an estimate of frogs densities. Tropical Zoology 20: 99–108.
- Santos TG, Rossa-Feres DC, Casatti L (2007) Diversidade e distribuição espaço-temporal de anuros em região com pronunciada estação seca no sudeste do Brasil. Iheringia, Série Zoologia 97(1): 37–49. https://doi.org/10.1590/S0073-47212007000100007
- Santos EJ, Conte CE (2016) Diversity of anurans in dry forest fragments of a subtropical region in Brazil. Anais da Academia Brasileira de Ciências 88 (3 Suppl.): 1923–1940. https://doi. org/10.1590/0001-3765201620150698

- Segalla MV, Caramaschi U, Cruz CAG, Garcia PCA, Grant T, Haddad CFB, Langone P (2016) Brazilian amphibians – List of species. http://www.sbherpetologia.org.br [Accessed on 15 November 2018]
- Silva J, Bates J (2002) Biogeographic patterns and conservation in the South American Cerrado: a tropical savanna hotspot. BioScience 52: 225–234. https://doi.org/10.1641/0006-3568(2002)052[0225:BPACIT]2.0.CO;2
- Silva JF, Fariñas MR, Felfili JM, Klink CA (2006) Spatial heterogeneity, land use and conservation in the cerrado region of Brazil. Journal of Biogeography 33: 536–548. https://doi.org/10.1111/j.1365-2699.2005.01422.x
- Silva RA, Martins IA, Rossa-Feres DC (2011) Environmental heterogeneity: Anuran diversity in homogeneous environments. Zoologia 28(5): 610–618. https://doi.org/10.1590/ S1984-46702011000500009
- Solbrig OT (1996) The diversity of the savana ecosystem. In: Solbrig OT, Medina EM, Silva JF (Eds) Biodiversity and Savanna Ecosystem Processes A Global Perspective. Springer-Verlag, Alemanha, 1–27.
- Strüssmann C, Prado CA, Uetanabaro M, Ferreira VL (2000) Amphibians and reptiles of selected localities in the southern Pantanal floodplains and neighboring Cerrado areas, Mato Grosso do Sul, Brasil. In: Willink PW, Chernoff B, Alonso LE, Montambault JR (Eds) A biological assessment of the aquatic ecosystems of the Pantanal, Mato Grosso do Sul, Brasil. Conservation International, Washington, 98–102.
- Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, Waller RW (2004) Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783– 1786. https://doi.org/10.1126/science.1103538
- Valdujo PH, Camacho A, Recoder RS, Júnior MT, Ghellere JMB, Mott T, Nunes PMS, Nogueira C, Rodrigues MT (2011) Anfíbios da Estação Ecológica Serra Geral do Tocantins, região do Jalapão, Estados do Tocantins e Bahia. Biota Neotropica 11(1): 251–262. https:// doi.org/10.1590/S1676-06032011000100025
- Valdujo PH, Silvano DL, Colli GR, Martins M (2012) Anuran Species Composition and Distribution Patterns in Brazilian Cerrado, a Neotropical Hotspot. South American Journal of Herpetology 7(2): 63–78. https://doi.org/10.2994/057.007.0209
- Vasconcelos TS, Rossa-Feres DC (2005) Diversidade, distribuição espacial e temporal de anfíbios anuros (Amphibia, Anura) na região noroeste do Estado de São Paulo, Brasil. Biota Neotropica 5(2): 137–150. https://doi.org/10.1590/S1676-06032005000300010
- Vasconcelos TS, Santos TG, Rossa-Feres DC, Haddad CFB (2009) Influence of the environmental heterogeneity of breeding ponds on anuran assemblages from southeastern Brazil. Canadian Journal Zoology 87: 699–707. https://doi.org/10.1139/Z09-058
- Vasconcelos TS, Santos TG, Haddad CFB, Rossa-Feres DC (2010) Climatic variables and altitude as predictors of anuran species richness and number of reproductive modes in Brazil. Journal of Tropical Ecology 26: 423–432. https://doi.org/10.1017/S0266467410000167
- Zar JH (2010) Biostatistical Analysis. 5° Edition. Prentice Hall, New Jersey, 662 pp.
- Zimmerman BL (1994) Audio Strip Transects. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LAC, Foster MS (Eds) Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington, 92–97.

Appendix I

Voucher specimens

Voucher specimens are deposited at the Herpetological Collection of the Universidade Federal do Amapá (UNIFAP), under the care of Carlos Eduardo Costa Campos (CEC-CAMPOS).

BUFONIDAE *Rhinella major* – CECCAMPOS 0747. *Rhinella* sp. – CECCAMPOS 0799-0800, 0805-0806. *Rhinela marina* – CECCAMPOS 0668.

HYLIDAE

Boana multifasciata – CECCAMPOS 0035, 0132, 0545. Boana punctate – CECCAMPOS 0050, 0130, 0550, 0554, 0600. Boana raniceps – CECCAMPOS 0486. Dendropsophus cf. walfordi – CECCAMPOS 0765-0769. Osteocephalus taurinus – CECCAMPOS 0676. Scinax fuscomarginatus – CECCAMPOS 0037. Scinax nebulosus – CECCAMPOS 0575-0580. Scinax ruber – CECCAMPOS 0745, 0747, 0761. Scinax x-signatus – CECCAMPOS 0321, 0683-0684. Trachycephalus typhonius – CECCAMPOS 0739-0740.

LEPTODACTYLIDAE

Pseudopaludicola boliviana – CECCAMPOS 1153. Adenomera hylaedactyla – CECCAMPOS 0047, 0548, 0560, 0609. Leptodactylus fuscus – CECCAMPOS 0586, 0589, 0748, 0749, 0762. Leptodactylus macrosternum – CECCAMPOS 0485, 0582. Leptodactylus pentadactylus – CECCAMPOS 0670, 0737. Leptodactylus podicipinus – CECCAMPOS 0048, 0049, 0606, 0753, 0772.

MICROHYLIDAE Elachistocleis helianneae – CECCAMPOS 0122, 0227.

PHYLLOMEDUSIDAE *Pithecopus hypochondrialis* – CECCAMPOS 0546, 0572, 0733.