RESEARCH ARTICLE



Biogeography and taxonomy of extinct and endangered monk seals illuminated by ancient DNA and skull morphology

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Abstract

Extinctions and declines of large marine vertebrates have major ecological impacts and are of critical concern in marine environments. The Caribbean monk seal, *Monachus tropicalis*, last definitively reported in 1952, was one of the few marine mammal species to become extinct in historical times. Despite its importance for understanding the evolutionary biogeography of southern phocids, the relationships of

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M. tropicalis to the two living species of critically endangered monk seals have not been resolved. In this study we present the first molecular data for *M. tropicalis*, derived from museum skins. Phylogenetic analysis of *cytochrome b* sequences indicates that *M. tropicalis* was more closely related to the Hawaiian rather than the Mediterranean monk seal. Divergence time estimation implicates the formation of the Panamanian Isthmus in the speciation of Caribbean and Hawaiian monk seals. Molecular, morphological and temporal divergence between the Mediterranean and "New World monk seals" (Hawaiian and Caribbean) is profound, equivalent to or greater than between sister genera of phocids. As a result, we classify the Caribbean and Hawaiian monk seals together in a newly erected genus, *Neomonachus*. The two genera of extant monk seals (*Monachus* and *Neomonachus*) represent old evolutionary lineages each represented by a single critically endangered species, both warranting continuing and concerted conservation attention and investment if they are to avoid the fate of their Caribbean relative.

Keywords

Ancient DNA, extinction, mitochondrial DNA, Panamanian Seaway, Phocidae, systematics

Introduction

"... he discovered a group of islets abounding with sea-fowl and marine animals. On one of them his sailors, in the course of a single night ... took fourteen sea-wolves, and killed a vast quantity of pelicans and other birds."

Washington Irving (1831) "Cruise of Ponce de Leon in search of the Fountain of Youth"

The Caribbean monk seal, Monachus tropicalis (Gray, 1850), first referenced on the New World voyages of Columbus in 1494 and Ponce de Leon in 1513, was one of the few large mammals to become extinct in the twentieth century. Until relatively recently, *M. tropicalis* was widely distributed in the Caribbean region (Figure 1), including along the Caribbean coasts of North, Central, and South America, and in the Bahamas and the Greater and Lesser Antilles (Timm et al. 1997, Adam 2004, Adam and Garcia 2003, McClenachan and Cooper 2008). Historical population estimates for the species ranged from 233,000-338,000 prior to the catastrophic decline of the species, caused by unrestricted hunting that increased throughout the nineteenth century (Mc-Clenachan and Cooper 2008). No well-documented sightings postdate 1952, and the species is widely regarded as extinct (Mignucci-Giannoni and Odell 2001, Adam and Garcia 2003, McClenachan and Cooper 2008). This is the only historical example of a marine mammal extinction in the tropics, and one of few species-level extinctions of marine mammals in the historical period, along with the Steller's sea cow (Hydrodamalis gigas, North Pacific, last recorded in 1768), the Japanese sea lion (Zalophus japonicus, East Asia, last recorded in 1951), and the Yangtze River dolphin or Baiji (Lipotes vexillifer, Yangtze River of China, probably extinct within the past decade) (Flannery and Schouten 2001, Wolf et al. 2007, Turvey 2009, Turvey et al. 2007).

There are two species of extant monk seals, both also classified in the genus *Monachus* Fleming, 1822, and both recognized by the IUCN as Critically Endangered species. The



Figure 1. Distributions of the three monk seal species. The range for the Caribbean monk seal is taken from Adam (2004) and is based on documented populations and archeological evidence. The range of the Mediterranean monk seal illustrates both historical (lighter shading) and current (darker shading) distributions.

Mediterranean monk seal, *Monachus monachus* (Hermann, 1779), occurred historically throughout the Mediterranean and Black Seas and along the Atlantic Coast of northern Africa (Figure 1). Today, a heavily fragmented global population of 350–450 individuals remains, dispersed throughout the Mediterranean and south-eastern North Atlantic (Sergeant et al. 1978, Pastor et al. 2007, Aguilar and Lowry 2013). The Hawaiian monk seal, *Monachus schauinslandi* Matschie, 1905, occurs throughout the Hawaiian island chain (Figure 1), with a current population of about 1000 animals (Lowry and Aguilar 2008, Schultz et al. 2009). Both of these extremely endangered species are threatened by many anthropogenic stressors, including mortality from hunting, entanglement in fishing gear, competition with fisheries for food, loss and disturbance of coastal habitats and breeding sites, oceanic pollution, and emerging diseases (Lowry and Aguilar 2008, Aguilar and Lowry 2013, Kovacs et al. 2012).

The relationship of the Caribbean monk seal to the two living species of *Monachus* has long been of interest to paleontologists, evolutionary biologists, and biogeographers (Repenning and Ray 1977, Wyss 1988, Bininda-Emonds and Russell 1996, Bininda-Emonds et al. 1999, Higdon et al. 2007). Morphological assessments have, to date, remained equivocal with regard to the relationships of *M. tropicalis* to the other monk seals. King (1956) was the first to compare the morphology of all three monk seal species in detail (though Matschie [1905] reported important earlier observations). Although King did not explicitly state a hypothesis regarding phylogenetic relationships within the genus, she noted a greater similarity between the skulls and dentitions of the Caribbean and Hawaiian monk seals than between either of these species and the Mediterranean monk seal (King 1956, King and Harrison 1961; also Kenyon and Rice 1959). Rice (1998) argued the opposite, suggesting greater similarity between the Med-

iterranean and Caribbean species. Quantitative cladistic analyses have suggested sistergroup relationships for the Caribbean monk seal to both the Mediterranean monk seal (Koretsky and Grigorescu 2002) and the Hawaiian monk seal (Bininda-Emonds and Russell 1996) on the basis of cranial and postcranial anatomy. Wyss's (1988) analysis of phocid morphology even suggested paraphyly of the genus, recovering 'Monachus' as a basal grade of phocids with 'M.' schauinslandi as the sister taxon to all other extant phocids. More recently, molecular phylogenetic analyses have confirmed monk seal monophyly, at least for the extant species, and their position in Monachinae as the likely sister group to Mirounga and the lobodontine seals of the southern oceans (Arnason et al. 1995, Ledje and Arnason 1996, Davis et al. 2004, Fyler et al. 2005, Fulton and Strobeck 2010a, 2010b). However, because the Caribbean monk seal is extinct and represented only by historical museum specimens (skins and skeletal material), rather than fresh frozen tissues, previous molecular phylogenies of phocids have not included the species. This has resulted in ambiguity regarding broader questions in pinniped evolution, such as the place of origin of the genus Monachus and the subfamily Monachinae (Ray 1976a, Deméré et al. 2003, Fyler et al. 2005, Fulton and Strobeck 2010a).

The initial objective of this study was to determine the phylogenetic placement of *M. tropicalis* and to estimate the timing of its divergence from the Hawaiian and Mediterranean monk seals, as well as from other phocids. Using ancient DNA methods (Willerslev and Cooper 2005), we successfully extracted and amplified a complete *cytochrome b* (hereafter *cyt*b) sequence from three *M. tropicalis* museum skins housed in the National Museum of Natural History, Smithsonian Institution (formerly United States National Museum, abbreviated USNM) and subjected these to phylogenetic analyses. Based on these results, as well as detailed examination of monk seal cranial morphology and considerations of divergence and biogeography, we recognize and name a new genus, *Neomonachus*, for the Caribbean and Hawaiian monk seals.

Materials and methods

Specimens examined

We examined all specimens of the three *Monachus* species in the collections of the USNM, which houses the only large collection of *Monachus tropicalis* (44 specimens, mostly represented by skins and/or skulls, most of which were collected by E.W. Nelson and E.A. Goldman at the turn of the twentieth century; Goldman 1951). The USNM also holds substantial material of *Monachus schauinslandi* for comparative study (54 specimens), but more limited material of *Monachus monachus* (one adult skull, likely a male, of unknown provenance, and one juvenile skull). We supplemented our observations of *Monachus* by studying material housed in the mammalogy collections of the Field Museum of Natural History, Chicago (FMNH), and the American Museum of Natural History, New York (AMNH) (including three skulls of *M. monachus*), and drawing from observations on specimens in the Natural History Museum (London)

(mainly *M. monachus*) as reported by King (1956). Dental measurements were collected by GJS using a Mitutuyo[®] digital caliper with 0.01 mm precision. Specimens shown in the photographic figures are USNM 219059 (*M. monachus*), USNM 181250 and 395761 (*M. schauinslandi*), and USNM 102534 and 102536 (*M. tropicalis*).

Samples, ancient DNA extraction, PCR and DNA sequencing

Several grams of dry skin were collected from six Caribbean monk seal museum specimens. All were originally collected in the Triangle Keys, a remote and tiny group of islands in Campeche, off the Yucatan Coast of Mexico. Two specimens (USNM 83711 and 83712) from the Triangle Keys were originally kept as captive animals on display at the National Zoological Park (Washington, D.C.), and transferred to the museum upon their death in 1897. The remaining specimens were collected by E.W. Nelson and E.A. Goldman, in June 1900 (Goldman 1951). Specimen catalog numbers and other information are provided in Table 1.

Historical DNA experiments were conducted in an ancient DNA laboratory dedicated to extractions and other pre-PCR procedures involving museum samples. The laboratory was equipped with plexiglass UV PCR hoods for extraction and PCR setup. All reagents and equipment in the lab were exclusively dedicated to ancient DNA experimental use. Modern DNA and PCR products never entered the room. All workstations were regularly UV-irradiated to avoid contamination. Extractions were performed with the Geneclean Kit for Ancient DNA (MP Biomedicals) as described by Roca et al. (2009). Primers for eleven PCR products ranging in size from 48–549 basepairs (bp) were designed to cover the 1140 bp of the monk seal cytb gene (primers are shown in Table 2, amplicon positions are shown in Suppl. material 1). PCR amplicons were produced by conventional and multiplex PCR. One extraction blank and one PCR water negative control were carried out for each PCR experiment. Conventional PCR amplifications were performed in 30.5µl volumes containing 1µl of 25mg/ml BSA (Fermentas), 1 µl of 10 pmol forward primer, 1µl of 10 pmol reverse primer, 22.5µl of Platinum PCR SuperMix High Fidelity Taq polymerase (Invitrogen), and 5µl of purified sample DNA. The thermal cycling conditions were 94°C for 4 min, followed by 60 cycles at 94°C for 30 s, at 55°C for 30 s, and at 72°C for 30 s, then finally 72°C for 5 min. Multiplex PCR amplifications were carried out in 59.5µl volumes that included 2µl of 25mg/ml BSA, 7.5µl of primer mix with primers of 1 pmol/µl concentration each, 45µl of Platinum PCR SuperMix High Fidelity Taq polymerase, and 5µl of purified sample. The PCR temperature profile was the same as in conventional PCR amplifications except that only 25 cycles were performed. Products of multiplex PCR were purified using QIAquick PCR purification kits (Qiagen) according to manufacturer instructions. Amplification of multiplex PCR products used the same cycling conditions as conventional PCR amplification except that 1µl of purified multiplex product was used as template. Amplification products were separated by electrophoresis on 3% agarose gels stained with GelRed (Biotium). Correct size products were cloned using the pGEM®-T Vector Systems Kit

USNM Number	Sex	Locality	Year	Collector
83711	Female	Bay of Campeche, Mexico	1897	National Zoological Park
83712	Male	Bay of Campeche, Mexico	1897	National Zoological Park
100358	Male	Triangle Keys, Bay of Campeche, Mexico	1900	EW Nelson and EA Goldman
100359	Female	Triangle Keys, Bay of Campeche, Mexico	1900	EW Nelson and EA Goldman
102527	Female	Triangle Keys, Bay of Campeche, Mexico	1900	EW Nelson and EA Goldman
102535	Female	Triangle Keys, Bay of Campeche, Mexico	1900	EW Nelson and EA Goldman

Table 1. Specimen information for Caribbean monk seals sampled in this study.

Table 2. List of primers used in this study. Asterisks indicate that the sequence extends over the 3' or 5' ends of the *cytb* gene. Amplicon sizes are shown in base pairs. The primer combinations are designated by numbers, e.g. P7.

Primer	Name	Sequence (5'-3')	Length (bp)
Ρ7	CYTB-MT-F1ATG ACC AAC AT(C/T) CGA AAA ACCYTB-MT-R1AAA GGC TGT (A/G)GT TGT GTC TG		149
P10	CYTB-MT-F4 CYTB-MT-R4	(T/C)TA CCA TGA GGA CAA AT(G/A) TC TG(T/G) ACT GCT (A/G)CT AGT GCT	153
P16	CYTB-MT-F1 CYTB-MT-R4	ATG ACC AAC AT(C/T) CGA AAA AC TG(T/G) ACT GCT (A/G)CT AGT GCT	549
P20	Flank-MT-F CYTB-FFla-R	CCA CCG TTG TAA TTC AAC TA GAT GAG TGA GTT ATT GAT AA	48*
P21	CYTB-MT-F9 CYTB-MT-R9	TAT TCC TAG CTA TAC ACT AC GTG AAT GTG TAG GAG CCG TA	144
P22	CYTB-MT-F10 CYTB-MT-R10	TAT CTG CTT ATA TAT ACA CGT A AGT AGA TTG GTG ATG ACG GT	135
P23	CYTB-MT-F11 CYTB-MT-R11	CAC TTC ATT ATA CCC TTC AT AAT GGG ATT TTG TCT GAG T	77
P24	CYTB-MT-F11 CYTB-MT-R5	CAC TTC ATT ATA CCC TTC AT CC(C/T) AGA ATG TCT TTA ATT GT	109
P32	CYTB-MT-F13 CYTB-MT-R13	CTC AGA CAA AAT CCC ATT TC GGG TTT GAT ATG TGG TGG	131
P40	CYTB-MT-F11 CYTB-MT-R13	CAC TTC ATT ATA CCC TTC AT GGG TTT GAT ATG TGG TGG	229
P42	CYTB-MT-F16 Flank-MT-R3	AGA CCC TGA CAA CTA TAC C GGT CTT GTA AAC CAA AAA CG	413*

(Promega) and JM109 High Efficiency Competent Cells (Promega) following manufacturer instructions. Ten clones of each PCR product were chosen and used in a colony PCR performed as described by Roca et al. (2009). PCR products from insert positive colonies were purified using QIAquick PCR purification kits and Sanger sequenced using standard M13 forward and reverse primers (StarSeq GmbH, Berlin). Aligned consensus sequences are shown for cyt*b* in Suppl. material 2. Consensus sequences, generated from 3-5 clones per amplicon from 2-3 replicate amplicons covering each base, were deposited in GenBank (accession JX853967). To enable a limited assessment of genetic variability within the Triangle Keys population prior to extinction, D-loop hypervariable region sequences were determined. Two fragments of the hypervariable region were successfully amplified and sequenced from 3 of the 6 extracted seals (Suppl. material 3).

Phylogenetic analysis

We integrated the Caribbean monk seal cytb sequence into an alignment of 35 previously sequenced caniform carnivore cytb sequences containing all extant phocid species (n = 18) and 17 outgroup taxa spanning 5 families (Table 3). We performed thorough phylogenetic analyses under the Maximum Likelihood (ML) optimality criterion using the POSIX-threads build of RAxML v7.5.3 (Stamatakis 2006) by running 100 searches starting from independent stepwise-addition maximum parsimony starting trees and the general time-reversible (GTR) substitution model with among-site rate heterogeneity modeled through the Γ distribution and four discrete rate categories (Lanave et al. 1984, Yang 1994). Node support was estimated with 1000 bootstrap pseudoreplicates (Felsenstein 1985) and the Shimodaira-Hasegawa-like nonparametric approximate likelihood-ratio test (a.k.a. SH-aLRT) (Shimodaira and Hasegawa 1999, Guindon et al. 2010). Bayesian inference of phylogeny was performed using MrBayes v3.2 (Ronquist et al. 2012). We performed two simultaneous runs of Metropolis-coupled Markov chain Monte Carlo each with four chains (one cold, three heated) of 10 million generations, sampling from the posterior distribution every 1000 steps. We ensured that both runs had converged on the target distribution and that adequate effective sample sizes had been obtained using Tracer v1.5. To determine the most appropriate partitioning scheme, we performed three separate analyses: 1) an unpartitioned analysis; 2) a two-partition analysis, with codon positions 1 and 2 treated as the first partition and the third codon position as the second partition; and 3) a threepartition analysis where each codon position was assigned to a distinct partition. Each partition was assigned a GTR + I + Γ model. Based on Bayes Factor comparison using the method of Suchard et al. (2001) implemented in Tracer (http://tree.bio.ed.ac.uk/ software/tracer), the three-partition scheme received decisive support, sensu Kass and Raftery (1995), over the two-partition ($\log_{10}BF = 23.24$) and unpartitioned ($\log_{10}BF =$ 277.6) schemes. Finally, we performed a maximum parsimony analysis (MP) using the DNAPARS program of the PHYLIP v3.6 package (Felsenstein 2005). All sites were treated as unweighted. Node support was evaluated through 1000 bootstrap pseudoreplicates mapped on a majority rule consensus tree.

Divergence time estimation

We estimated divergence times using BEAST v1.7.4 (Drummond et al. 2012). Fulton and Strobeck (2010a) noted that phocid divergence time estimates derived from mito-

Family	Binomial	Common name	GenBank accession no.	Source		
	Phoca largha	Spotted seal	X82305	Arnason et al. (1995)		
Family Phocidae Otariidae Otariidae	Phoca vitulina	Harbor seal	X82306	Arnason et al. (1995)		
	Pusa sibirica	Baikal seal	AY140977	Palo and Vainola (2006)		
	Pusa hispida	Ringed seal	X82304	Arnason et al. (1995)		
	Pusa caspica	Caspian seal	AY140978	Palo and Vainola (2006)		
	Halichoerus grypus	Gray seal	NC001602	Arnason and Gullberg (1993)		
Phocidae	Cystophora cristata	Hooded seal	X82294	Arnason et al. (1995)		
	Histriophoca fasciata	Ribbon seal	X82302	Arnason et al. (1995)		
	Pagophilus groenlandicus	Harp seal	X82303	Arnason et al. (1995)		
	Erignathus barbatus	Bearded seal	AY170104	Yoder et al. (2003)		
	Hydrurga leptonyx	Leopard seal	AY377323	Davis et al. (2004)		
	Leptonychotes weddellii	Weddell seal	AY377324	Davis et al. (2004)		
	Ommatophoca rossii	Ross seal	AY377322	Davis et al. (2004)		
	Lobodon carcinophagus	Crabeater seal	AY377321	Davis et al. (2004)		
	Neomonachus schauinslandi	Hawaiian monk seal	X72209	Arnason and Gullberg (1993		
	Neomonachus tropicalis	Caribbean monk seal	JX853967	this study		
	Monachus monachus	Mediterranean monk seal	AY377327	Davis et al. (2004)		
	Mirounga leonina	Southern elephant seal	AY377326	Davis et al. (2004)		
	Mirounga angustirostris	Northern elephant seal	AY377325	Davis et al. (2004)		
Family Phocidae Phocidae Otariidae Otariidae Mustelidae Ursidae Canidae	Arctocephalus australis	South American fur seal	AY377329	Davis et al. (2004)		
	Arctocephalus forsteri	New Zealand fur seal	X82293	Arnason et al. (1995)		
	Arctocephalus gazella	Antarctic fur seal	X82292	Source Arnason et al. (1995) Arnason et al. (1995) Palo and Vainola (2006) Arnason et al. (1995) Palo and Vainola (2006) Arnason et al. (1995) Palo and Vainola (2006) Arnason et al. (1995) Arnason et al. (1995) Arnason et al. (1995) Arnason et al. (1995) Arnason et al. (2003) Davis et al. (2004) Arnason et al. (1995) Arnason et al. (1995) Arnason et al. (1995) Arnason et al. (2007) Arnason et al. (2007)		
Otariidae	Otaria flavescens	South American sea lion	AY377328	Davis et al. (2004)		
	Zalophus californianus	California sea lion	X82310	Arnason et al. (1995)		
Family Phocidae Phocidae Otariidae Odobenidae Mustelidae Ursidae Canidae	Eumetopias jubatus	Steller sea lion	DQ145021	Harlin-Cognato et al. (2006)		
	Callorhinus ursinus	Northern fur seal	NC008415	Arnason et al. (2006)		
Odobenidae	Odobenus rosmarus	Walrus	X82299	Arnason et al. (1995)		
	Meles meles	Eurasian badger	NC011125	Arnason et al. (2007)		
Mustelidae	Gulo gulo	Wolverine	NC009685	Arnason et al. (2007)		
	Mustela nivalis	Least weasel	JX853967 this study AY377327 Davis et al. (2004) AY377326 Davis et al. (2004) AY377325 Davis et al. (2004) AY377326 Davis et al. (2004) AY377327 Davis et al. (2004) AY377329 Davis et al. (2004) X82293 Arnason et al. (1995) X82292 Arnason et al. (1995) AY377328 Davis et al. (2004) X82310 Arnason et al. (1995) DQ145021 Harlin-Cognato et al. (2006) X82299 Arnason et al. (2006) X82299 Arnason et al. (2007) NC008415 Arnason et al. (2007) NC011125 Arnason et al. (2007) NC009685 Arnason et al. (2007) HM106319 Yu et al. (2011) NC003426 Delisle and Strobeck (2002) HQ685963 Keis et al. (2013)			
	Ursus americanus	American black bear	NC003426	Delisle and Strobeck (2002)		
Ursidae	Ursus arctos	Brown bear	HQ685963	Keis et al. (2013)		
	Ailuropoda melanoleuca	Giant panda	NC009492	Peng et al. (2007)		
	Vulpes vulpes	Red fox	NC008434	Arnason et al. (2006)		
Canidae	Nyctereutes procyonoides	Raccoon dog	GU256221	Chen and Zhang (2012)		
	Canis lupus	Gray wolf	AY170103	Yoder et al. (2003)		

Table 3. List of species and associated GenBank accession information used in phylogenetic analysis of *cytb* sequence data.

chondrial sequences alone resulted in older ages, in some cases as much as 5 million years older, than were estimated from nuclear only or nuclear plus mitochondrial data. Such an artifact is problematic for our purposes because such dramatic differences in diver-

gence time estimates will result in substantially different interpretations of the biogeographic context for Caribbean monk seal evolution. For the purposes of divergence dating in this study, we therefore integrated our Caribbean monk seal cyt*b* sequence into the alignment of 15 nuclear genes plus complete mitochondrial genome sequence data from Fulton and Strobeck (2010a), kindly provided to us by Tara Fulton. GenBank accession numbers for sequences used are listed in Appendix S1 of Fulton and Strobeck (2010a). Prior to adding the Caribbean monk seal sequence, we removed the third codon position, which Fulton and Strobeck (2010a) found to show a saturated substitution rate in their analyses, thus having the potential to overestimate branch lengths. The alignment was partitioned by nuclear gene, and all mitochondrial sequences (codon positions 1 and 2) treated as a single, additional partition. Substitution models followed those determined through Akaike Information Criterion (Akaike 1974) comparison in MrModel-Test (https://github.com/nylander/MrModeltest2) by Fulton and Strobeck (2010a), and specified in Appendix S2 of Fulton and Strobeck (2010a).

Some authors have questioned the appropriateness of using taxa with incomplete sequences in phylogenetic and divergence time inferences (Lemmon et al. 2009), noting that doing so can result in misleading topological and branch length estimates (but see Roure et al. 2013 for a comment on this simulation study). However, a number of other studies have suggested that even highly incomplete taxa can have a positive influence in phylogenetic analysis (e.g., Huelsenbeck 1991, Wiens and Moen 2008, Wiens and Morrill 2011, Wiens and Tiu 2012). Ideally, we would have sequenced at least one nuclear locus for our Caribbean monk seal sample for inclusion in phylogenetic analysis. However, due to the sequence divergence from other seals and relatively poor quality of the DNA extracted, this would represent a major undertaking that would have a high chance of failure by PCR-based approaches from 100 year-old museum samples and would be unlikely to alter the conclusions of our study. Ultimately, we opted to include the Caribbean monk seal cytb sequence in a larger pinniped alignment of nuclear and mitochondrial sequence data for two reasons. First, accurate divergence time inference is key to understanding the biogeographic context for the evolution of New World monk seals. Given the results presented by Fulton and Strobeck (2010a), we simply cannot rely on divergence time estimates from one mitochondrial locus alone, across all pinnipeds, for a sound evolutionary interpretation. Second, previous studies suggest that incomplete sequences do not have a substantial impact on branch length estimation when the model of sequence evolution is correctly specified (Wiens and Moen 2008), and that they are less problematic when the branch leading to the sparsely sampled taxon is relatively short (Roure et al. 2013). Because our divergence time analysis, like that of Fulton and Strobeck (2010a), uses a relaxed, uncorrelated molecular clock, with substitution models unlinked across loci, the impacts of the large amount of missing data for the Caribbean monk seal should be limited. In contrast, the benefit of our approach is that it effectively uses divergence times for extant phocids inferred from the more complete nuclear + mitochondrial alignment as a framework for constraining the range of possible divergence time estimates for the Caribbean monk seal from its closest living relatives.

We performed joint estimation of topology and divergence times in BEAST v1.7.4 (Drummond et al. 2012) by using the same set of node priors as in Fulton and Strobeck (2010a; see their Table 2, with reasoning in the supplementary information) but with two additions: a prior for crown Canidae was applied to the node uniting the most recent common ancestor of *Canis lupus* and *Vulpes lagopus*, and a prior for the first appearance of *Eumetopias* and *Zalophus* was applied to the node uniting *Eumetopias jubatus* and *Arctocephalus* spp., following ages and justifications provided in Slater et al. (2012). We ran two independent Markov chains for 50 million generations, sampling from the posterior distribution every 10,000 generations. After visually checking for convergence of the chains in Tracer, we conservatively removed the first 25% of samples as burn-in and produced a maximum clade credibility tree from the retained sample.

Sequence divergence among phocids

Fulton and Strobeck (2010b) noted that pairwise genetic distances between the two extant monk seal species were greater than the distances between any pair of species within extant genera. They further observed that the magnitude of genetic divergence between the two monk seals was more comparable to tribal-level differences among other phocids. To further examine variation in sequence divergence within *Monachus* and among phocid species in general, we replicated their analyses incorporating our Caribbean monk seal sequence. Following the same approach taken by Fulton and Strobeck (2010b), we computed logdet pairwise genetic distances from the aligned phocid cyt*b* sequences and summarized values at interspecific, generic, and tribal levels within Phocinae and Monachinae. Distances were computed using the dist.dna() function in the APE (Paradis et al. 2004) package for R (R Development Core Team 2012).

Results

Sequence retrieval

The Caribbean monk seal cytb gene was generated from a 112-year-old specimen (USNM 100358) from multiple extractions and overlapping PCR amplicons (Suppl. material 1). The consensus sequence of the 1140 bp of cytb represents at least duplicate coverage of every base by an independent amplicon. The results were consistent across all experiments, except for two nucleotide positions that differed in more than one PCR. Those were G-A changes and are most likely due to template deamination on the complementary strand (Hofreiter et al. 2001). The correct base at the two positions was resolved with further independent PCRs that indicated that at both positions, G was the correct nucleotide, as A only appeared among clones in one amplicon. The

consensus sequence displayed 90% identity to that of *Monachus schauinslandi* and high similarity to other phocid sequences. The fact that the overlapping sequences used to create the consensus sequence matched in the overlaps and no premature stop codons were identified in any amplicon supports the conclusion that the cytb sequence represents organellar mtDNA and not a nuclear-derived mtDNA sequence (Bensasson et al. 2001). The hypervariable region sequences determined from three Caribbean monk seal individuals were identical for both non-overlapping fragments (Suppl. material 3), possibly indicating limited genetic diversity in one of the last surviving populations of the species at the turn of the twentieth century.

Phylogenetic analysis

Phylogenetic analyses of the complete cytb sequences under MP, ML, and BI (Figure 2, Suppl. material 4) recovered a monophyletic monk seal clade (BS-MP = 45%, BS-ML = 70%, SH-aLRT = 0.78, PP = 0.93), with a well-supported subclade of New World species (BS-MP = 96%, BS-ML = 100%, SH-aLRT = 0.99, PP = 1.00). Our analyses therefore indicate that the Caribbean and Hawaiian monk seals are more closely related to each other than either is to the Mediterranean monk seal, supported by 9 synapomorphic, non-synonymous changes. The rest of our cytb tree topology is generally consistent with earlier studies of phocid relationships. One notable exception concerns relationships at the base of Monachinae, where we recovered Mirounga (the elephant seals) as the sister lineage to other monachines (Figure 2). Recent studies utilizing both nuclear and mitochondrial loci have revealed that Monachus is sister to Mirounga + Lobodontini (Fyler et al. 2005, Fulton and Strobeck 2010a, 2010b). The (Mirounga, (Monachini, Lobontini)) relationship is weakly supported in our analyses, however (BS-ML = 55%, SH-aLRT = 0.73, PP = 0.8), and likely reflects inadequacy of cytb data alone to resolve deeper, rapid divergence events (Fyler et al. 2005). The more common branching order of (Monachini, (Mirounga, Lobontini)) was recovered in our parsimony analyses (Suppl. material 4), but with even weaker support (BS-MP = 29%).

Divergence time estimation

We estimated the divergence of the Caribbean and Hawaiian monk seals at 3.67 Mya (95% HPD = 1.90-5.45 Mya). Node age estimates throughout the rest of the chronogram derived from analysis of the nuclear + mitochondrial genome data are consistent with those recovered by the original analysis of Fulton and Strobeck (2010a) (Figure 3). The Mediterranean-New World monk seal divergence is dated at 6.30 Mya (95% HPD = 4.98-7.64 Mya) in our analyses, slightly older than, but broadly overlapping with the age of 5.48 Mya (95% HPD = 3.93-7.13 Mya) reported by Fulton and Strobeck (2010a).



Figure 2. Maximum likelihood phylogram inferred from *cytb* sequence data using the GTR + Γ_4 substitution model. Node support is expressed as the percent proportion of 1000 bootstrap pseudoreplicates that agree with the bipartitions on the best ML tree (above internode branches) as well as the aLRT SHlike score (below internode branches). Support values above 80% for both measures are shown. Black boxes indicate nodes recovered with >0.88 posterior probability in Bayesian analyses. The scale bar indicates the number of substitutions per site.



Figure 3. Time-calibrated phylogeny of the seals estimated from combined nuclear and mitochondrial data. Time scale is in millions of years before present. Note that the chronogram has been pruned to show only true seals and immediate pinniped outgroups. Node bars show the 95% HPD intervals for divergence time estimates and mean ages are labeled for the two divergence times within the monk seals. Labeling at the top indicates water circulation through the Central American Seaway, the circle and associated wavy blue lines indicate a period during which water circulation periodically ceased and resumed but a shallow seaway remained open.

Sequence divergence

Pairwise genetic distances incorporating the Caribbean monk seal (Figure 4) confirm the findings of Fulton and Strobeck (2010b). Genetic distances between currently



Figure 4. Genetic distances between currently recognized taxonomic units within Phocidae derived from logdet distances for *cytb*. Distances within: **a** *Phoca* **b** *Pusa* **c** *Phoca* versus *Halichoerus* **d** *Pusa* versus *Halichoerus* **d** *Pusa* versus *Halichoerus* **e** *Phoca* versus *Pusa* **f** *Histriophoca* versus *Pagophilus* **g** Phocini **h** Phocinae **i** *Monachus* **j** *Mirounga* **k** Lobodontini, and **I** Monachini.

recognized generic lineages within the subtribe Phocina (*Phoca, Pusa*, and *Halichoerus*) are more similar to species-level, rather than generic-level, distinctions in other phocid lineages (perhaps an indication that this lineage is generically 'oversplit'). Within *Monachus*, our analyses reveal that sequence divergence between all three species is of a similar magnitude and equivalent to tribal-level divergence in other phocine and monachine taxa.

Discussion

Systematics and evolution of the Caribbean monk seal

Our results provide the first molecular evidence for the phylogenetic placement of the Caribbean monk seal. The monophyly of *Monachus* has been questioned on the basis of morphology (Wyss 1988), but molecular studies, which have not included the Caribbean monk seal, have confirmed the sister relationship of the two extant monk seal species (Arnason et al. 2006, Ledje and Arnason 1996, Davis et al. 2004, Fyler et al. 2005, Fulton and Strobeck 2010a, 2010b). Our analyses confirm the monophyly of *Monachus*, albeit with relatively deep divergences among all three Recent species (see below).

The exact relationships of the extinct Caribbean monk seal have previously been unclear, with sister relationships to both extant monk seal species suggested on the basis of morphology (Bininda-Emonds et al. 1999, Koretsky and Grigorescu 2002). Our finding of a sister relationship between the Caribbean and Hawaiian monk seals, and our estimate for their associated divergence time, have important implications for understanding the biogeographic context of monachine evolution. Extant monachine seals are primarily Southern Ocean specialists, with some species, including members of Monachus, extending to tropical and mid-latitude portions of the Atlantic and Pacific. This has led to some confusion regarding the origin of the subfamily as a whole, as well as the processes giving rise to the disjunct distribution of the recent species of Monachus (e.g., Fyler et al. 2005, Fulton and Strobeck 2010a). Our results suggest that an eastern mid-Atlantic origin for Monachus with subsequent dispersal to the western Atlantic in the common ancestor of the two New World species is plausible (e.g., Deméré et al. 2003). However, a western Atlantic origin with dispersal to the eastern Atlantic in the lineage leading to Monachus monachus would be equally parsimonious based on our results, and attempts to quantitatively assess these hypotheses using Dispersal-Extinction-Cladogenesis models (Ree and Smith 2008, data not shown) were equivocal regarding the center of origin of Monachus, Monachinae, and Phocidae. Fortunately, monachines possess a rich fossil record from Middle Miocene and Pliocene deposits of Europe (Koretsky and Grigorescu 2002), the northwestern Atlantic (Ray 1976a, Deméré et al. 2003), and the Pacific coast of South America (Walsh and Naish 2002, Valenzuela-Toro et al. 2013, Amson and Muizon 2013). Ray (1976a, 1976b) noted that monachines were the dominant pinnipeds of the North Atlantic until the Pliocene, and suggested that the distribution of extant monk seals could be explained by extinction of high latitude species and their replacement by phocine seals. Integra-

tion of fossil monachines into the complete molecular phylogeny of Recent phocids that we have generated here will undoubtedly play an important role in robustly resolving these biogeographic questions (e.g., Wood et al. 2013).

Our analyses confirm that the closure of the Central American seaway after the completion of the Panamanian Isthmus could have played a prominent role in explaining the evolution and distributions of the two New World monk seals. Although the phylogenetic placement of the Caribbean monk seal has been uncertain until now, this significant geological and biotic event has traditionally been invoked to explain the divergence of New World *Monachus* species through vicariance (e.g., Ray 1976a, Repenning and Ray 1977, Repenning et al. 1979, Deméré et al. 2003, Fyler et al. 2005, Fulton and Strobeck 2010a). Exact dates for the final formation of the Panamanian land bridge, which led to the Great American Biotic Interchange in terrestrial ecosystems, are uncertain but estimates usually range from about 4–2 Mya (e.g., Coates et al. 1992, Coates and Obando 1996, Bartoli et al. 2005, Jackson and O'Dea 2013; though see also Montes et al. 2012). Oxygen isotope data from the foraminiferal record provide valuable information about oceanic salinity levels on either side of the forming land bridge prior to this time and, by extension, indicate the degree of water flow and connectivity between the Pacific and Atlantic oceans (Haug et al. 2001) that would be

essential for dispersal of marine mammal populations. Divergence in estimated salinity levels from Pacific and Caribbean sites indicates that intermediate water transfer from the Pacific to the Atlantic began to reduce approximately 4.5-4.0 Mya, but that a shallow surface water connection remained, causing low-salinity Pacific surface waters to flow into the Caribbean sea, until at least 3.0 Mya (Haug et al. 2001, Bartoli et al. 2005). Convergence in foraminiferal δ^{18} O values at 3.3 and 3.8 Mya further indicate that intermediate water transfer resumed, albeit temporarily, during this window (Bartoli et al. 2005), leading to full potential for dispersal between Atlantic and Pacific Oceans by marine mammals. We estimated a mean divergence time for the two New World monk seals of 3.67 Mya, well within this period of reduced connectivity between the Pacific and Atlantic (Figure 3), suggesting that vicariance is a viable explanation for the divergence of the two species. The common ancestor of New World monk seals may have been more broadly distributed throughout the shallow Central American Seaway during the Late Pliocene, although to the best of our knowledge there is no fossil evidence for the presence of *Monachus* along the Pacific shoreline. Populations of this ancestral form would likely have also used small islands that ultimately became part of Panama as haul-out sites. The final closure of the Seaway at 2.5–2.0 Mya created allopatric populations, split between the two oceans, that would give rise to the modern Caribbean and Hawaiian species. The upper 95% HPD for the age of the most recent common ancestor of *M. tropicalis* and *M. schauinslandi* in our analyses was 1.90 Mya, suggesting that divergence postdating the closure of the seaway (e.g., via dispersal around the southern tip of South America) is unlikely.

Generic taxonomy: definition of a second monk seal genus

Though all three monk seals are currently classified in a single genus, *Monachus*, the split between New World monk seals and the Mediterranean monk seal is far older than the basal divergence within any other currently recognized modern seal genus (Figure 3) and genetic distances between *Monachus* species exceed those among other phocid tribes (Figure 4). Wyss (1988) advocated for the splitting of *Monachus* into multiple genera once the relationships among monk seals were better resolved. Although our examination of specimens did not reveal sufficient characters to warrant supra-specific distinction between the Caribbean and Hawaiian monk seals, we did find a large number of characters differentiating the two New World monk seals from the Mediterranean monk seal. Tying together the genetic, temporal, and morphological evidence, we here propose a new genus for the New World species.

All previous generic-level names applied to monk seals have as their type species the Mediterranean monk seal, *M. monachus* (Hermann, 1779), and are thus synonyms of *Monachus* Fleming, 1822, the earliest generic name erected with that species as its type. These synonyms include *Pelagios* F. Cuvier, 1824 (including its various subsequent spellings and the replacement name *Rigoon* Gistel, 1848), *Pelagocyon* Gloger, 1841, and *Heliophoca* Gray, 1854, as well as Herrera's (1899) eccentric (and invalid)

usage of *Mammonachus* (Gray 1866, Thomas 1895, Palmer 1904, King 1956, Wozencraft 2005). Neither the Caribbean nor the Hawaiian monk seal has been designated as the type species of any previously erected genus-level name, so a new generic name is required.

Neomonachus Slater & Helgen, gen. n.

http://zoobank.org/1F643A9A-4D26-44DD-B7D7-C3EB9BE3804B http://species-id.net/wiki/Neomonachus

Type species. Monachus schauinslandi Matschie, 1905 (endemic to the Hawaiian Islands).

Other included species. A second species, Monachus tropicalis (Gray, 1850) (endemic to the Caribbean region, recently extinct). We note here, as an aside, that an earlier specific epithet, antillarum Gray, 1849, has often been included in the synonymy of tropicalis, where it is identified either as a partial synonym (e.g., Allen 1880: 708, 1887:3, Adam 2004:1) or a nomen nudum (Wozencraft 2005:598), or simply listed as a synonym without comment (Wozencraft 1993:331, Berta and Churchill 2012:219). However, Gray (1849) in fact used this name to describe Cystophora antillarum, based on a juvenile male specimen of a Hooded seal, supposedly from Jamaica (Allen 1880, Gill 1866), and the name is not a nomen nudum. It is clear that the skin of the Caribbean monk seal that Gray later used to describe *Phoca tropicalis* (Gray 1850), also from Jamaica, was not part of his hypodigm of antillarum, to which he explicitly attributed a single Cystophora skin and skull (Gray 1849, 1850; Allen 1887:postscript). Thus the name *antillarum* does not correctly belong in the synonymy of *N. tropicalis* (it is neither a partial synonym nor a *nomen nudum*). It is instead simply a junior synonym for the Hooded seal, Cystophora cristata (which occasionally occurs as a Caribbean vagrant: Mignucci-Giannoni and Odell 2001, Ward et al. 2013). The only additional name that correctly belongs in the technical synonymy of tropicalis is the junior synonym [Phoca] wilkianus (Gosse 1851), described from the Pedro Keys, south coast of Jamaica, soon after Gray's (1850) description of tropicalis (see Allen 1880).

Etymology. The new generic name combines the Greek *Neo*- (new), with *Mona-chus*, the genus name previously used for all monk seals. The name references both the recognition of a new genus within the monk seals and its New World (Western Hemisphere) distribution.

Morphological diagnosis. Species of *Neomonachus* can be distinguished from *Monachus* in their smaller average body size and in lacking a white ventral patch on the pelage (in both adults and young) (Adam 2004). Species of *Neomonachus* possess a narrower and more gracile skull than *Monachus*, with relatively poorly developed sagittal and occipital crests in even the largest males (Figure 5). The rostrum is low and elongate with a conspicuous diastema between C1 and the first upper premolar (P1). In *Monachus*, the diastema is lacking and the anterior edge of P1 may be positioned medially to the canine (Figures 5, 6). The antorbital process of the maxilla (Figure 7) is present in *Monachus* but is extremely reduced or absent in *Neomonachus*



Figure 5. Lateral views of crania of a *Monachus monachus* b *Neomonachus schauinslandi*, and c *Neomonachus tropicalis*. Arrows indicate the more developed occipital crest and zygomatic arches, and deeper snout of *Monachus* compared to *Neomonachus* species.

(King 1956). The nasals are relatively narrow and posteriorly extended in *Neomonachus* compared to *Monachus* (Figure 7). The zygomatic arch is dorso-ventrally shallow and the jugal portion lacks a well-developed masseteric margin ventrally or orbital margin superiorly (the zygomatic arch is robust and both margins are well-defined in *Monachus*) (Figure 5). The pterygoid shows a conspicuous, laterally flared hamular process in *Neomonachus* (King 1956) that may be spatulate (*N. schauinslandi*) or hook-like (*N. tropicalis*); the process is absent or small and medially inflected in *Monachus* (Figure 8).

In ventral view, the morphology of the petromastoid (petrosal-mastoid) complex in relation to the auditory bulla in *Neomonachus* is diagnostic in comparison to *Monachus*. King (1966) noted that having the petrosal visible within the posterior lacerate



Figure 6. Ventral views of palates of **a** *Monachus monachus* **b** *Neomonachus schauinslandi*, and **c** *Neomonachus tropicalis*. The tooth row of *Monachus* is more crowded, likely as a result of the shorter rostrum, and this results in a more obliquely oriented set of post-canine teeth and the lack of a diastema between the upper canine and the first premolar. In *Neomonachus*, there is a distinct diastema between C1 and P1, and the post-canine teeth are arranged more linearly. The upper incisor arcade of *Monachus* is slightly parabolic due to the posterior placement of the lateral incisors, and the anterior premaxilla appears slightly curved. In *Neomonachus*, the incisor arcade is linear and the anterior premaxilla is straight.



Figure 7. Dorsal view of rostra of **a** *Monachus monachus* **b** *Neomonachus schauinslandi*, and **c** *Neomonachus tropicalis. Monachus* exhibits a well-developed antorbital process on the maxilla, immediately inferior to the fronto-maxillary suture. The process is reduced or absent in *Neomonachus*. The nasals of *Monachus* are short and triangular, tapering smoothly posteriorly to produce a point at their union. The nasals of *Neomonachus* are longer and do not taper smoothly.

foramen was a feature that united *Monachus* and the phocines, although Ray (1976b) pointed out that it is difficult to distinguish the boundaries of the petrosal and mastoid (petromastoid complex) in the posterior lacerate foramen and that this character was



Figure 8. Ventral views of crania of a *Monachus monachus* b *Neomonachus schauinslandi*, and c *Neomonachus tropicalis*, showing the pterygoid region. *Neomonachus* exhibits a well-developed, laterally flared pterygoid hamulus that is visible in dorsal view. The hamulus may be spatulate (*N. schauinslandi*) or hook-like (*N. tropicalis*). The hamular process is absent or medially flared in *Monachus*, and is not visible in dorsal view.

far more variable within lobodontines than King had estimated. He argued that a better standard for delineating this character state uniting *Mirounga* and the lobodontines is a bulla in near contact or complete contact with the exoccipital. We agree with Ray's



Figure 9. Posteroventral view of the basicranium and left bulla in **a** *Monachus monachus* **b** *Neomonachus schauinslandi*, and **c** *Neomonachus tropicalis*. The bulla of *Monachus* is bordered posteriorly by a ventrally expanded posterior portion of the petro-mastoid complex. The petrosal abuts the bulla's posterior wall and in ventral view forms the entire lateral and anterolateral border of the posterior lacerate foramen. In *Neomonachus*, the posterior part of the petrosal is visible in the posterior lacerate foramen but remains superior to the bulla. In ventral view, this gives the impression that the anterior border of the posterior lacerate foramen is formed entirely by the bulla. The posterior carotid canal opens posteroventrally in *Monachus*. This apparently results from a relatively complete "ring-like" opening, formed by the bulla. This form of opening is apparent in subadult and juvenile *Monachus*, suggesting that it is not dependent on ontogenetic development or the robusticity of the *Monachus* cranium relative to *Neomonachus*. In contrast, the posterior carotid canal of *Neomonachus* opens directly posteriorly, the opening being an incomplete ring and the dorsal border formed by a flattening of the bulla, perhaps resulting from the bulla's extension over the petrosal.

assessment, but we note that the configuration of the petromastoid complex and bulla with respect to the posterior lacerate foramen is more complex within "Monachus" (i.e. sensu lato) than has been previously described. In particular, the petromastoid of Monachus monachus is clearly ventrally inflated, such that it protrudes below the rim of the posterior lacerate foramen, forming its entire lateral border (Figure 9a). Furthermore, the ventral expansion of the petromastoid almost completely excludes the flat posterior edge of the bulla from the anterior margin of the posterior lacerate foramen. This morphology, which is also present in the fossil taxon Pliophoca, has been proposed as synapormorphic for Monachini (Amson and de Muizon 2013). However, in Neomonachus, the tapering posterior margin of the bulla lies completely ventral to the petromastoid, the posterior border of which is visible within the neurocranium through the posterior lacerate foramen (Figure 9: b and c). Ray also noted that the posterior carotid foramen opens in full view in Monachus (sensu lato) but is partially concealed on the medial bulla wall in phocines (Ray 1976b). Our observations show that, for *Neomonachus*, the posterior carotid canal opens directly posteriorly, with a flattened dorsal roof formed by excavation of the caudal entotympanic (Figure 9). In Monachus, the canal opens postero-ventrally due to a more complete, ring-like opening. These character-state differences are clearly developed even in juvenile individuals, indicating that they are not the outcome of ontogenetic variation.



Figure 10. Plots of mean upper (**a**) and lower (**b**) relative post-canine tooth size. Relative tooth size is computed by dividing the mesio-distal length of each tooth by the length of the 3rd premolar (which is typically largest) in the same row.

The upper incisor arcade of *Neomonachus* is sublinear, while that of *Monachus* appears slightly parabolic due to a more posteriorly set I3 (King 1956; Figure 6). The upper post-canine toothrow of *Neomonachus* is arranged more linearly than in *Monachus*, where the teeth are obliquely oriented. In specimens of *Neomonachus* with unworn dentitions, both upper and lower premolars and first molar possess low, blunt central cusps and two posterior accessory cusps, as compared with a high, pointed central cusp and a single posterior accessory cusp for *Monachus*. In both *Neomonachus* and *Monachus*, p3 is the largest of the lower teeth. However, in *Monachus*, lower post-canine tooth size decreases in the order p3, p2, p4, m1, p1, while the lower teeth of *Neomonachus* decrease in the order p3, p4, p2, m1, p1; and p4 may be larger than p3 in some individuals (Figure 10).

The mandible of *Neomonachus* is long and slender compared with that of *Monachus*, and the coronoid process is lower and less broad antero-posteriorly (King 1956; Figure 11). The mandibular foramen is anteriorly displaced and lies at the termination of a shallow, antero-ventrally oriented sulcus that begins below the level of the mandibular notch. In *Monachus*, the foramen opens directly at this level. The insertion of the pterygoid muscles is relatively undefined in *Neomonachus* as compared to the markedly expanded area evident in *Monachus* (Figure 11).

Conclusion

We obtained the first DNA sequence data from the recently extinct Caribbean monk seal. Based on phylogenetic analysis and divergence time estimation, we revealed that the Caribbean and Hawaiian monk seals form a well-supported monophyletic New



Figure 11. Medial view of right dentaries of **a** *Monachus monachus* **b** *Neomonachus schauinslandi*, and **c** *Neomonachus tropicalis*. The mandibular foramen is situated inferior to the mandibular notch in *Monachus*, and opens immediately to the medial surface of the ramus. In *Neomonachus*, the foramen is anteriorly displaced and is set in a groove or sulcus that extends from inferior to the mandibular notch. Also note the expanded rugose area for insertion of the pterygoid muscles in *Monachus*. This region is poorly developed in *Neomonachus*.

World clade that diverged from the Mediterranean monk seal lineage ~ 6.3 Mya. Our results further implicate the closure of the Central American Seaway in the Late Pliocene as a driver of divergence between the Caribbean and Hawaiian monk seals,

supporting a classical hypothesis in pinniped evolutionary biology. In combination, our morphological examinations of museum specimens and our phylogenetic analyses indicate that the substantial evolutionary divergence and trenchant morphological distinctions between the Mediterranean monk seal and the New World monk seals are similar to or greater than levels of molecular and morphological divergence between other sister phocid genera. Because no genus-level name has previously been proposed for the New World monk seals, we name and diagnose a new genus, *Neomonachus*, to accommodate the endangered Hawaiian and extinct Caribbean monk seals, leaving the Mediterranean monk seal as the sole species of *Monachus*.

Our findings and conclusions have broad significance for the two surviving species of monk seal. Because the Caribbean monk seal is already extinct, the elevation of the New World species to a new genus means that both extant monk seals (*Monachus monachus and Neomonachus schauinslandi*) are the sole remaining representatives of their respective genera—extremely distinctive seal lineages representing deep, independent evolutionary histories. Both species are critically endangered, with an extant populations of about 1000 individuals for *N. schauinslandi* and a heavily fragmented and widely distributed population of fewer than 500 individuals for *M. monachus*. Formal recognition of two genera for the living monk seals better indicates their true evolutionary, ecomorphological, and taxonomic uniqueness within the context of pinniped evolution, and this taxonomic change grants even greater poignancy to all efforts to conserve these endangered species.

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Supplementary material I

Amplicons covering *cyt*b in this study.

Authors: Dirk-Martin Scheel, Graham J. Slater, Sergios-Orestis Kolokotronis, Charles W. Potter, David S. Rotstein, Kyriakos Tsangaras, Alex D. Greenwood, Kristofer M. Helgen Data type: Picture

- Explanation note: Sequence of the *cyt*b gene and the resulting PCR amplicons with length in number of base pairs (bp). Asterisks indicate that the sequence extends over the 3' or 5' border of the target sequence.
- 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: doi: 10.3897/zookeys.409.6244.app1

Supplementary material 2

Alignment of *N. tropicalis cyt*b with extant monk seal *cyt*b sequences.

Authors: Dirk-Martin Scheel, Graham J. Slater, Sergios-Orestis Kolokotronis, Charles W. Potter, David S. Rotstein, Kyriakos Tsangaras, Alex D. Greenwood, Kristofer M. Helgen Data type: Picture

- Explanation note: The extinct Caribbean monk seal sequence was used as a reference. Dots indicate identity to the reference. Differences are shown as the base change relative to the reference. Numbering starts from the first base of the ATG start codon.
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Link: doi: 10.3897/zookeys.409.6244.app2

Supplementary material 3

Alignment of three *N. tropicalis* D-loop hypervariable region sequences (from USNM 100358, 102527, and 102534).

Authors: Dirk-Martin Scheel, Graham J. Slater, Sergios-Orestis Kolokotronis, Charles W. Potter, David S. Rotstein, Kyriakos Tsangaras, Alex D. Greenwood, Kristofer M. Helgen Data type: Picture

- Explanation note: The *N. schauinslandi* sequence was used as a reference. Dots indicate identity to the reference. Differences are shown as the base change relative to the reference. Numbering starts at the first base after the primer closest to the 5' end. The X symbols indicate the break between the two amplicons that are approximately 200 bp apart. Sequences were generated from consensus sequences of 3–5 individual PCR product clones. Several products were cloned and sequenced from more than one amplicon to confirm that the differences observed were not DNA damage related or due to sequencing errors.
- 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: doi: 10.3897/zookeys.409.6244.app3

Supplementary material 4

Fifty percent majority-rule consensus tree based on 1000 bootstrap pseudoreplicates generated using the maximum parsimony phylogenetic optimality criterion.

Authors: Dirk-Martin Scheel, Graham J. Slater, Sergios-Orestis Kolokotronis, Charles W. Potter, David S. Rotstein, Kyriakos Tsangaras, Alex D. Greenwood, Kristofer M. Helgen Data type: Picture

- Explanation note: Values at nodes indicate the proportion of bootstrap trees (>50%) for which a particular bipartition was recovered.
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RESEARCH ARTICLE



Reevaluation of the odd chrysidid genus Atoposega Krombein (Hymenoptera, Chrysididae, Amiseginae)

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+ http://zoobank.org/ADC91A84-7D87-41E4-A4B3-87BA1041D7DD

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Abstract

The south Asian amisegine genus *Atoposega* Krombein, 1957, is reevaluated. Three new species, *A. rufithorax*, *A. striata* and *A. thailandica* are described from Thailand and the previously described species, *A. lineata* (Krombein, 1957) from Borneo, *A. rieki* (Krombein, 1957) from Myanmar and *A. simulans* Kimsey, 1986 from Malaysia are redescribed. The species, *A. decorata* Kimsey, 1995, was found to lack the generic characters diagnostic for *Atoposega*. *Atoposega* is only known from females.

Keywords

Mahinda, Perissosega, Chiang Mai, Thailand

Introduction

Female *Atoposega* Krombein, 1957 are among the more striking members of the chrysidid subfamily Amiseginae. They are brightly colored and elaborately sculptured, with long, spine-like propodeal teeth (a feature shared with female *Mahinda* Krombein, 1983) and often banded wings. However, *Mahinda* females are strongly brachypterous. Thus far *Atoposega* is only known from females. The only other genus with the same Rs vein configuration is *Perissosega* Krombein, 1983 from Sri Lanka, which is known from both sexes. *Perissosega* females are fully winged and have a well-developed

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Figure 1. Distribution map of *Atoposega* species. The location of *rieki* is centrally placed in-country as the actual locality is unknown.

transverse frontal carina. No male amisegines are known that have the distinctively angulate Rs vein seen in male and female *Perissosega* and in female *Atoposega*.

Species of *Atoposega* are known from southern Asia (Fig. 1). The intensive survey of Hymenoptera of Thailand, a U.S. National Science Foundation project, NSF No. 0542864, headed by Michael Sharkey revealed several additional species of *Atoposega*. The one species outside of this region, *Atoposega decorata* Kimsey, 1995, from New Caledonia lacks many of the generic traits that characterize *Atoposega* and is probably not congeneric. Thus this species is not included in this study, and will be treated in a separate paper.

Nothing is known of the biology of *Atoposega* species, although it is assumed that they are parasites of walking stick eggs like other members of the subfamily.

Materials and methods

Specimens were studied from the following institutions and/or these are the type repositories: AEI – American Entomological Institute, Gainesville, Florida, USA; BME – Bohart Museum of Entomology, University of California, Davis, USA; MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MNHN
– Museúm National d'Histoire Naturelle, Paris, France; QSBG – Queen Sirikit Botanic Garden, Chiang Mai, Thailand; USNM – U. S. National Museum of Natural History, Washington, D. C., USA.

Terminology used below follows that of Kimsey and Bohart (1991). Proportions of the flagellomeres are based on the greatest length versus the broadest part of the article, generally the apical margin.

Taxonomy

Genus Atoposega Krombein

http://species-id.net/wiki/Atoposega

Atopogyne Krombein, 1957: 184. Type: Atopogyne lineata Krombein, 1957:186. Nec Forel 1911. Original designation

Atoposega Krombein, 1960: 33. Replacement name for Atopogyne Krombein.

Diagnosis. Female *Atoposega* most closely resemble those of *Mahinda* Krombein based on the acute or spine-like propodeal angles and mesopleuron with-well developed omaulus. Female Atoposega differ from Mahinda as they are fully winged (all known Mahinda are strongly brachypterous), the hindcoxa has with two longitudinal carina (one or none in *Mahinda*), and the mesopleuron has a dorsally carinate and U-shaped posteromedial groove (a narrow, parallel-sided longitudinal groove in *Mahinda*). In addition *Mahinda* females have two sharp submedial angles above the posterior propodeal declivity, which do not occur in Atoposega. Perissosega females are fully winged, but unlike Atoposega and Mahinda have a transverse frontal carina, and lack an omaulus. Atoposega can be distinguished from other amisegine genera by these characters, and by the dentate tarsal claws, malar space with a vertical sulcus, frons without transverse carina, vertex without longitudinal welt, pronotum with posteromedial longitudinal pit, and short sulcus and pit adjacent to lateral posterior lobe, mesopleuron without scrobal sulcus, metanotal dorsal enclosure usually V-shaped, propodeum with two dorsomedial decumbent angles and posterior declivity smooth and impunctate, with longitudinal medial carina, and forewing with an arcuate Rs vein.

Generic description. Head: occipital carina well-developed, visible laterally; eye with tiny sparse setulae, encircled by carina; scapal basin deep, wide and coarsely cross-ridged; malar space with vertical groove; female flagellum short, fusiform and flattened on one surface. Mesosoma: pronotum with posteromedial groove and deep pit before lateral lobe, 0.8–0.9× as long as combined lengths of scutum, scutellum and metano-tum; scutum with notauli deep and narrow, without parapsides; mesopleuron evenly punctate, omaulus well-developed, scrobal sulcus absent, posteromedial fossa U-shaped, carina edged; metanotum elongate, subequal in length to scutellum, with triangular medial enclosure; propodeum dorsal surface bending abruptly to posterior declivity, lateral angles long, spike-like; hindcoxa with two longitudinal, dorsobasal carinae; tarsal

claw with large medial tooth; female fully winged; forewing R1 clearly indicated, medial vein arising before cu-a, Rs extended at abrupt angle by dark streak; wings densely setose, often banded. Metasoma: sternum I produced into large basal keel.

Distribution. *Atoposega* species have been collected in Myanmar, Borneo, Thailand and Malaysia.

Key to the species of Atoposega

1	Metasomal tergum II with dense fine longitudinal scratches laterally, extending length of tergum, joining posteriorly and appearing U-shaped (as in Fig. 7)2
_	Metasomal tergum II with apicolateral patch of dense fine longitudinal
	scratches, only extending part of tergal length, not joining posteriorly or ap-
	pearing U-shaped
2	Midocellus 1.0-1.5 midocellar diameters from nearest eye margin; wing
	banded, with contrasting bands of dark brown alternating with untinted or
	whitish bands; Myanmar <i>rieki</i> Krombein
_	Midocellus 2 or more midocellar diameters from nearest eye margin; wing
	unbanded, brown-tinted
3	Metanotum punctate without medial ridge; flagellomere II dark brown; Thai-
	land rufithorax sp. n.
_	Metanotum areolate with medial ridge; flagellomere II partly to entirely
	whiteh Theiland
	wintish; finaliand striata sp. n.
4	Flagellomere I 4× as long as broad; hindocellus less than one diameter from near-
4	Flagellomere I 4× as long as broad; hindocellus less than one diameter from near- est eye margin in dorsal view; forewing with contrasting bands of dark brown
4	Flagellomere I 4× as long as broad; hindocellus less than one diameter from near- est eye margin in dorsal view; forewing with contrasting bands of dark brown alternating with untinted or whitish bands; Thailand
4	Flagellomere I 4× as long as broad; hindocellus less than one diameter from near- est eye margin in dorsal view; forewing with contrasting bands of dark brown alternating with untinted or whitish bands; Thailand
4	Flagellomere I 4× as long as broad; hindocellus less than one diameter from near- est eye margin in dorsal view; forewing with contrasting bands of dark brown alternating with untinted or whitish bands; Thailand
4 - 5	Flagellomere I 4× as long as broad; hindocellus less than one diameter from near- est eye margin in dorsal view; forewing with contrasting bands of dark brown alternating with untinted or whitish bands; Thailand
4 - 5	Flagellomere I 4× as long as broad; hindocellus less than one diameter from near- est eye margin in dorsal view; forewing with contrasting bands of dark brown alternating with untinted or whitish bands; Thailand
4 - 5	Flagellomere I 4× as long as broad; hindocellus less than one diameter from near- est eye margin in dorsal view; forewing with contrasting bands of dark brown alternating with untinted or whitish bands; Thailand
4 - 5	Flagellomere I 4× as long as broad; hindocellus less than one diameter from near- est eye margin in dorsal view; forewing with contrasting bands of dark brown alternating with untinted or whitish bands; Thailand
4 - 5 -	Flagellomere I 4× as long as broad; hindocellus less than one diameter from near- est eye margin in dorsal view; forewing with contrasting bands of dark brown alternating with untinted or whitish bands; Thailand
4 - 5	Flagellomere I 4× as long as broad; hindocellus less than one diameter from near- est eye margin in dorsal view; forewing with contrasting bands of dark brown alternating with untinted or whitish bands; Thailand

Atoposega lineata (Krombein)

http://species-id.net/wiki/Atoposega_lineata Figures 2, 8

Atopogyne lineata Krombein, 1957:186. Holotype female; Borneo: Sandakan (USNM).

Material examined. Malaysian Borneo: Sandakan. Only the type series has been seen.



Figures 2-6. Front view of female Atoposega face, with one antenna removed.

Diagnosis. This species most closely resembles *simulans* and less so *thailandica*. All lack the dense U-shaped scratches on metasomal tergum II. *Atoposega lineata* and *thailandica* both have banded wings, but *lineata* can be distinguished by the hindocellus separated from the eye margin by more than one diameter and flagellomere I less than 4× as long as broad.

Female description. Body (Fig. 8): length 6 mm. Head: face (Fig. 2); scapal basin cross-ridged medially; frons with punctures contiguous; malar space 3 midocellus diameters long; head 0.8× as long as wide; midocellus 2.6–2.7 midocellus diameters from ocular margin in front view; ocelli arranged in triangle broader between hindocelli than between hind and midocelli; hindocellus separated from ocular margin by 1.5 ocellar diameters in dorsal view; clypeus somewhat convex apically; subantennal distance 0.8 midocellus diameters: flagellomere I length 3× breadth; flagellomeres II and III 0.7× as long as broad; flagellomere XI 1.2× as long as broad. Mesosoma:

pronotal, scutal and scutellar punctures large, contiguous, separated by longitudinal ridges; pronotum and scutum subequal in length; scutum with notauli well-developed anteriorly; mesopleural punctures contiguous; metanotum 1.3× as long as scutellum, medial enclosure coarsely areolate, with medial ridge; propodeal dorsal surface coarsely areolate, posterior surface with medial longitudinal carina, enclosure smooth, impunctate on either side; forefemur with tiny contiguous punctures dorsally, punctures becoming separated by 1 puncture diameter ventrally; hindfemur with tiny contiguous punctures dorsally, punctures becoming larger and contiguous ventrally, with longitudinal impunctate band ventrally; metapleuron and propodeal side coarsely cross-ridged. Metasoma: tergum I polished, impunctate; tergum II polished, impunctate medially from anterior to posterior margins, laterally with dense, tiny punctures and fine, dense longitudinal scratches; terga III-IV polished with scattered tiny punctures; sternum II with punctures tiny, 5–10 puncture diameters apart, III-IV punctures tiny, contiguous to 0.5 puncture diameters apart. Color: head black; mesosoma red; propodeum black dorsally and posteriorly, laterally and lateral tooth partly to completely red; wings banded, dark brown-tinted, with un-tinted band across wing at Rs and near base; antenna with scape, pedicel red, flagellomere I paler red dorsally, browner ventrally, flagellomeres II-IX dark brown; legs red, midcoxae and hindfemora may have brown lateral spot; metasoma black with faint metallic green tints.

Atoposega rieki (Krombein)

http://species-id.net/wiki/Atoposega_rieki

Atopogyne rieki Krombein 1957:187. Holotype female; "Birmanie" (Myanmar) (PARIS).

Material examined. Type unavailable for study; Myanmar.

Diagnosis. Atoposega rieki most closely resembles rufithorax and striata based on the presence of fine dense longitudinal scratches on metasomal tergum II that join posteriorly, appearing broadly U-shaped. It can be distinguished from those species by the narrower subantennal distance, midocellus separated from the eye margin by less than two midocellar diameters, and banded wings.

Female description (based on Krombein 1957). Body: length 6 mm. Head: face scapal basin transversely ridged medially; frons with punctures deep, contiguous; malar space 3.5 midocellus diameters long; head 0.9× as long as wide; midocellus 1.3 midocellus diameters from ocular margin; ocelli arranged in isosceles triangle; hindocellus separated from ocular margin by 0.9 diameter; clypeus apicomedially indented; subantennal distance 0.7 midocellus diameters: flagellomere I length 3.7× breadth; flagellomere II as long as broad. Mesosoma: pronotal, scutal and scutellar punctures 0.3–0.5 puncture diameter apart; pronotum 0.6× as long as scutum, scutellum and metanotum combined; scutum with notauli well-developed



Figures 7-11. Lateral view of female Atoposega.

anteriorly, broader posteriorly; mesopleuron with punctures contiguous to 0.5 puncture diameter apart; metanotum 0.9× as long as scutellum; hindfemur minutely, finely rugulose ventrally. Metasoma: tergum I smooth, impunctate in medial half, lateral fourth finely, longitudinally carinate; tergum II with basal triangular, finely punctate area, laterally with dense, longitudinal carinae joined posteriorly into U-shape; terga III and IV finely, densely punctate; sterna II and III with large, dense punctures. Color: head black; antenna dark brown, except scape, pedicel and flagellomere I paler basally and apex of flagellomere I blackish; flagellomeres II-XI blackish; thorax red, except dorsal and posterior face of propodeum black; legs brown, except coxae, trochanters, femora and ibiae narrowly basally red, hindtibial apex and venter of hindfemur dark brown; metasoma shiny black, with faint green tints on terga I-II; wing membrane with alternating pale or brown bands.

Atoposega rufithorax Kimsey, sp. n.

http://zoobank.org/56C23D93-6921-4396-9EAA-DB97766835C3 http://species-id.net/wiki/Atoposega_rufithorax Figures 3, 7, 9

Type material. Holotype female: Thailand: Chaiyaphum Prov., Tat Tone NP, Phu hang sing, 15°58.723'N, 102°2.231'E, 290m, Malaise trap, 19–26/vii/2006, T. Jaruphan & O. Budsawong, T226 (QSBG). Paratypes: 9 females: 1 female: dry dipterocarp forest, 15°59.037'N, 102°2.103'E, 250m, Malaise trap, 25–27/vi/2006, M. Sharkey, T10; 1 female: Khonkaen Prov., Nam Pong NP, 16°37.377'N, 102°34.454'E, Malaise Trap, 5–12/vii/2006, K, Jaidee, T106; 1 female: 12–19/vii/2006, K. Jaidee, T110; 1 female: 16°37.201'N, 102°34.481'E, Malaise trap, 5–12/vii/2006, K. Jaidee, T107; 1 female: 12–19.vii.2006, K. Jaidee, T112; 1 female: Prachuab Khiri Khan Prov., Khao Sam Roi Yot NP, Laem Sala beach, 12°12.234'N, 100°0.767'E, Malaise trap, 10–17/viii/2008, Yai & Amnad, T3010; 1 female: Phetchabun Prov., Nam Nao NP, hill evergreen forest, 16°44.387'N, 101°34.531'E, 838m, pan trap, 28–29/v/2007, N. Hongyothi & L. Janteab, T2424; 1 female: helicopter landing ground, 16°43.113'N, 101°35.134'E, 889 m, Malaise trap, 10–17/vii/2006, N. Hongyothi, T273; 1 female: Khao Kho NP office, 16°39.55'N, 101°8.123'E, 230m, Malaise trap, 12–19/vii/2006, S. Chatchumnan & S. Singtong, T167 (QSBG, BME).

Diagnosis. This is one of three species, including *striata* and *rieki*, with fine dense longitudinal carinae on the sides of metanotal tergum II that join posteromedially. It can be distinguished from those species by the lack of an elevated, medial metanotal ridge, and the scutellum roughly planar with the metanotum and separated from the metanotum by a deep notch in side view.

Female description. Body (Fig. 9): length 3.5–4.5 mm. Head: face (Fig. 3); scapal basin finely, cross-ridged medially without discrete, longitudinal medial ridge; frons with punctures contiguous; malar space 3.5 midocellus diameters long; head 0.8× as long as broad in front view; midocellus 2.0–2.3 midocellus diameters from ocular margin; hindocelli further apart than midocellar-hindocellar distance; hindocellus separated from ocular margin by 0.7 hindocellar diameter; clypeus slightly concave apicomedially, punctures small, irregular; subantennal distance 0.8–0.9 midocellus diameters: flagellomere I length 5× breadth; flagellomere II 0.9× as long as broad; flagellomere III 0.7× as long as broad; flagellomere XI 1.5× as long as broad. Mesosoma: pronotal, scutal and scutellar punctures 0.5–1.0 puncture diameter apart, finely, densely striate between punctures; pronotum and scutum subequal in length; scutal notauli deep for entire length of scutum; mesopleuron without depression from pronotal lobe to scrobe, punctures large, deep, contiguous; metanotum 0.7× as long as scutellum, medial enclosure with large irregular punctures, without medial ridge; scutellum and metanotum subplanar in lateral view; propodeal dorsal surface coarsely areolate, posterior surface with carina margined medial enclosure, with longitudinal medial ridge; metapleuron and propodeal side with fine dense cross-ridging; forefemur with contiguous, tiny punctures dorsally and ventrally; hindfemur with dense tiny punctures dorsally, ventrally punctures becoming larger and reticulate. Metasoma: tergum I medial half impunctate, lateral fourth densely longitudinally striate, tergum II medially with impunctate band extending half length of tergum, becoming densely finely punctate extending laterally and becoming finely longitudinally striate, striae joining posteriorly becoming U-shaped (Fig. 7); terga III and IV with dense tiny, contiguous striatiform punctures; sterna II-IV with small punctures separated by 0.5–1.0 puncture diameters. Color: head black; scape bicolored, red to light brown ventrally, blackish dorsally; pedicel and flagellomere I pale red to brown; flagellum blackish; thorax and legs red, becoming paler ventrally, including all or most of lateral propodeum and propodeal teeth, propodeum black dorsally and posteriorly, hindtibia blackish to dark brown, with pale joints; metasomal segments black, terga with metallic bluish green tints, sternum I may be brownish; wing membrane brown-tinted, unbanded.

Etymology. The name refers to the red coloration of the thorax.

Atoposega simulans Kimsey

http://species-id.net/wiki/Atoposega_simulans Figure 4

Atoposega simulans Kimsey 1986:153. Holotype female; Malaysia: Pasoh Forest Res., Negri Sembilan (AEI).

Material studied. Malaysia: Negri Sembilan; Thailand: Loei Prov., Phu Ruea NP; Prachuap Khiri Khan Prov., Khan Sam Rui Yot NP; Chaiyaphum Prov., Tai Tome NP, Pha Bin Ngan NP; Ubon Ratchathani, Pha Taem NP; Khon Kaen Prov., Nam Pong NP; Phetchabun Prov., Khao Kho NP, Nam Nao NP; Sakon Nakhon Prov., Phu Pham NP; in the months of December, January and April-October; 22 females were examined including the holotype (BME, AEI).

Diagnosis. This species most closely resembles *lineata* based on dimensions of the flagellomere I, the lack of longitudinal striae on metasomal tergum II and the hindocellus separated from the nearest eye margin by more than one diameter. *Atoposega simulans* can be distinguished from *lineata* by the lack of lateral longitudinal scratches on metasomal tergum I and evenly brown-tinted wings.

Female description. Body: length 2.5–5.0 mm. Head: face (Fig. 4); scapal basin with dense, coarse cross-ridges medially; frons with punctures large, contiguous; malar space 3.0–3.5 midocellus diameters long; head width 1.2–1.3× length; midocellus 2.5 midocellus diameters from ocular margin; ocelli arranged in broad triangle; hindocellus separated from ocular margin by 1.2 diameters in dorsal view; clypeus flattened apically; subantennal distance 1 midocellus diameter long; flagellomere I length 3× breadth; flagellomere II 0.6× as long as broad. Mesosoma: pronotal, scutal and scutellar punctures large, coarse and contiguous; pronotum half as long as combined lengths of scutum, scutellum and metanotum; scutum with notauli deeper posteriorly than anteriorly; mesopleuron with large, deep, contiguous punctures;

metanotum 0.6–0.8× as long as scutellum, medial enclosure areolate, with strong medial, longitudinal ridge; propodeal dorsal surface coarsely areolate, posterior surface with medial enclosure with medial, longitudinal ridge and coarse cross-ridging laterally; metapleuron and propodeal side with coarse cross-ridging; forefemur with tiny, contiguous punctures dorsally, ventrally punctures 2-3 puncture diameters apart; hindfemur with tiny, contiguous punctures dorsally, ventrally punctures separated by 0.5–1.0 puncture diameters, with broad, longitudinal impunctate, polished band medially; metapleuron and propodeal side coarsely cross-ridged. Metasoma: terga I and II polished and impunctate medially, lateral third with fine longitudinal scratches and punctures, punctures 1 puncture diameter apart, scratches merging posteriorly forming U-shape; terga III-IV with dense, contiguous tiny punctures; sternum II with tiny, widely separated punctures 5-10 puncture diameters apart; sterna III-IV punctures tiny, dense and contiguous to 0.5 puncture diameters apart. Color: head black; scape light brown; pedicel and flagellomere I whitish, except apex of flagellomere I blackish; flagellomeres II-XI blackish; thorax red, except dorsal and posterior face of propodeum black; legs and coxae red, except foretarsomeres, hindtibal apex and venter of hindfemur dark brown; metasoma shiny black, with faint green tints on terga I-II; wing membrane brown-tinted, with dark bands across wing at medial vein and apex of Rs alternating with pale bands.

Atoposega striata Kimsey, sp. n.

http://zoobank.org/1BF8067D-553A-4D70-B7AE-423832348296 http://species-id.net/wiki/Atoposega_striata Figures 5, 10

Type material. Holotype female: Thailand: Chaiyaphum Prov., Tat Tone NP, Phu hang sing 15°58.723'N, 102°02.231'E, Malaise trap, 19–26/vii/2006, T. Jaruphan & O. Budsawong, T1226 (QSBG). Paratypes. 13 females: 1 female: dry dipterocarp forest, 15°59.037'N, 102°2.103'E, 250m, Malaise trap, 29/vi/2006, L. Ittichan, T30; 1 female: entrance to Pa Eang waterfall, 15°57.520'N, 101°54.442'E, 297m, Malaise trap, 12–19/x/2006, T. Jaruphan, T681; 1 female: 15°58.538'N, 102°02.153'E, 280m, pan trap, 6-7/i/2007, T. Jaruphan & O. Budsawong, T1552; 1 female: Thung Dok Kra Jeow, dipterocarp forest, 15°38.208'N, 101°23.556'E, 720m, Malaise trap, 7-13/i/2007, K. Sa-nog & B. Adnafai, T1458; 2 females: Khonkaen Prov., Nam Pong NP, 16°37.377'N, 102°34.454'E, Malaise Trap, 12-19/vii/2006, K. Jaidee, T111; 1 female: Prachuab Khiri Khan Prov., Khao Sam Roi Yot NP, Laem Sala beach, 12°12.234'N, 100°0.767'E, Malaise trap, 10-17/viii/2008, Yai & Amnad, T3010; 1 female: 17-24/viii/2008, Yai & Sorat, T3016; 1 female: 200 m s checkpoint 1, 12°12.789'N, 99°58.662'E, Malaise trap, 28/ix-5/x/2008, Y. Amnad, T4102; 1 female: Loei Prov., Phu Kradueng NP, Nampong/Pong Neep forest unit, 16°56.59'N, 101°41.61'E, 273m, Malaise trap, 19–26/iv/2008, T. Phatai, T5130;

1 female: forest protection unit 5, 16°50.66'N, 101°41.5'E, 420m, Malaise trap, 12–19/vi/2008, T. Phatai, T5048; 1 female: Ubon Ratchathani Prov., Pha Taem NP, west of Huay Pok forest unit, 15°37.321'N, 105°36.982'E, 419m, Malaise trap, 6–13/x/2006, T719; 1 female: Sakon Nakhon Prov., Phu Phan NP, behind office, 17°3.543'N, 103°58.452'E, 312m, Malaise trap, 8–14/vii/2006, W. Kongnara, T197 (QSBG, BME).

Diagnosis. This species is closest to *rufithorax* based on dimensions of the flagellomeres, length of the subantennal distance and lack of a posterior propodeal enclosure. It can be distinguished from *rufithorax* by the presence of an elevated, medial metanotal ridge, the scutellum elevated above metanotum and separated from the metanotum by a deep notch in side view, and clypeal apex truncate not broadly rounded as in *rufithorax*.

Female description. Body (Fig. 10): length 3–5 mm. Head: face (Fig. 5); scapal basin coarsely, cross-ridged medially, with medial ridge; frons with punctures contiguous; malar space 3.5 midocellus diameters long; head 0.8× as long as wide in front view; midocellus 2.5 midocellus diameters from ocular margin; hindocelli further apart than midocellar-hindocellar distance; hindocellus separated from ocular margin by 0.8× hindocellar diameter; clypeus flat apicomedially, punctures small, irregular; subantennal distance 1.0-1.2 midocellus diameters: flagellomere I length 3.8× breadth; flagellomere II as 0.8× as long as broad; flagellomere III 0.6× as long as broad, flagellomere XI 1.6x as long as broad. Mesosoma: Pronotal, scutal and scutellar punctures 0.5–1.0 puncture diameter apart, finely, densely striate between punctures; pronotum as long as scutum in length; scutal notauli deeper posteriorly than anteriorly, extending entire length of scutum; mesopleuron without depression from pronotal lobe to scrobe, punctures large, deep, contiguous; metanotum 0.9× as long as scutellum, medial enclosure areolate, with strongly elevated medial ridge; propodeal dorsal surface coarsely areolate, posterior surface with medial enclosure with elevated marginal carina particularly well-developed dorsally, with longitudinal medial ridge and transverse ridges; metapleuron and propodeal side densely cross-ridged; forefemur and hindfemur densely punctate-reticulate ventrally. Metasoma: terga I and II polished and impunctate medially, lateral third with fine longitudinal scratches and punctures, punctures 1 puncture diameter apart, scratches merging posteriorly forming U-shape; terga III-IV with dense, contiguous tiny punctures; sterna II-IV with dense small punctures 0.5–1.0 puncture diameters apart, punctures smaller and somewhat denser on III-IV. Color: head black; scape bicolored, red to light brown ventrally, blackish dorsally; pedicel and flagellomere I pale red to brown; flagellum blackish; thorax and legs red, becoming paler ventrally, including all or most of lateral propodeum and propodeal teeth, hindtibia black, with pale joints; propodeum black dorsally and posteriorly; metasomal segments black, terga with metallic green tints, sternum I may be brownish; wing membrane brown-tinted.

Etymology. The species name refers to the fine longitudinal scratches on the dorsum of the mesosoma.

Atoposega thailandica Kimsey, sp. n.

http://zoobank.org/55B5117A-FE01-44D8-AEAD-F81381415DB5 http://species-id.net/wiki/Atoposega_thailandica Figures 6, 11

Type material. Holotype female: Thailand: Chiang Mai Prov., Doi Chiangdao NP Water reservoir, 19°24.419'N, 98°55.237'E, 549m, Malaise trap, 11–18.ix.2007, S. Jugsu & A. Watwanich, T5686 (QSBG). Paratypes: 6 females: 1 female: Doi Inthanon NP, 700 m, 18°32N 98°36E, Malaise trap, 8–15/vii/2006, Y. Areeluck, T62; 1 female: Phetchabun Prov., Nam Nao NP, pine forest/Sambon 1, 16°42.47'N, 101°35.26'E, 872m, Malaise trap, 5–12/iv/2007, L. Janteab, T4948; 1 female: helicopter landing ground, 16°43.113'N, 101°35.134'E 889m, Malaise trap 17–24/vii/2006, N. Hongy-othi leg. T276; 1 female, Loei Prov., Phu Ruea NP, 17°27.829'N, 101°21.36'E, 691m, pan trap, 5–6/xii/2006, P. Tumtip, T1254; 1 female: Sakon Nakhon Prov., Phu Phan NP, 17°9.824'N, 103°54.511'E, 199m, Malaise trap, 25–31/x/2006, W. Kongnara, T709; 1 female: Chaiyaphum Prov., Pa Hin Ngam NP, car park at Tung Dok Grajeaw, 15°38.438'N, 101°23.576'E 780m, pan trap 7–8/vii/2006, Kratae Sanog & Buakaw Adnafai, T325 (QSBG, BME).

Diagnosis. This species most closely resembles *lineata* and *simulans* based on the lack of fine dense U-shaped striae on metasomal tergum II. The banded wings resemble those of *rieki* and *lineata*. *Atoposega thailandica* can be distinguished from these species by the combination of flagellomere I 4× as long as broad (versus 3×) and hindocellus separated by less than 1 diameter from the nearest eye margin.

Female description. Body (Fig. 11): length 5–6 mm. Head: face (Fig. 6); scapal basin cross-ridged medially; frons with punctures contiguous; malar space 2.6 midocellus diameters long; head 0.9× as long as wide; midocellus 2.2 midocellus diameters from ocular margin; hindocelli slightly further part than hindocelli and midocellus; hindocellus separated from ocular margin by 0.8 diameter; clypeus coarsely punctate and flattened apically; subantennal distance 0.9 midocellus diameters long; flagellomere I length 4× breadth; flagellomere II 0.5–0.6× as long as broad; flagellomere III 0.4× as long as broad; flagellomere XI 1.8× as long as broad. Mesosoma: pronotal, scutal and scutellar punctures large, contiguous, separated by longitudinal ridges; pronotum and scutum subequal in length; scutum with notauli deeper posteriorly than anteriorly; mesopleuron with large, contiguous punctures; metanotum 0.8× as long as scutellum, medial enclosure coarsely areolate, with medial ridge; propodeal dorsal surface coarsely areolate, posterior surface with numerous cross-ridges on either side of longitudinal medial ridge; metapleuron and propodeal side coarsely cross-ridged; hindcoxa with two dorsal, longitudinal carinae, merging basally, elevated into basal tooth or angle; forefemur ventrally with tiny, contiguous punctures; hindfemur ventrally with longitudinal polished impunctate band. Metasoma: tergum highly polished, medial two-thirds impunctate, laterally with zone of small punctures, separated by 0.5-1.0 puncture diameters; tergum II medial third polished impunctate on anterior half of tergum, lateral third punctate, with punctures separated by 0.5–1.0 puncture diameters,

becoming slightly striatiform laterally; terga III-IV with dense, small, contiguous punctures; sterna II-IV with punctures separated by 0.5–1.0 puncture diameter, punctures largest on II becoming progressively smaller on subsequent sterna. Color: head black; scape bicolored, red to light brown ventrally, blackish dorsally; pedicel and flagellomere I pale red to brown; flagellum blackish; mesosoma and legs red, becoming paler ventrally, including all or most of lateral propodeum and propodeal teeth, hindtibia black with pale joints; propodeum black dorsally and posteriorly; metasomal segments black, terga with brassy tints, sternum I may be brownish; wing membrane bicolored, membrane and setae dark brown tinted, with broad pale band across wing at stigma.

Etymology. The species is named after the country of collection.

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RESEARCH ARTICLE



Supplement to the revision of the genus Eremosaprinus Ross, 1939 (Coleoptera, Histeridae, Saprininae): new distributional data and description of a new species from Arizona, U.S.A.

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Abstract

A new species of the genus *Eremosaprinus* Ross, 1939, *E. warneri*, is described from southeastern Arizona, USA, and incorporated into the identification key for the genus. Description of the new species is supplemented with SEM micrographs and drawings of sensory structures of the antenna and male genitalia. New distribution data on four species, *E. distinctus* Lundgren, 1992, *E. hubbardi* (Wenzel, 1939), *E. minimus* Tishechkin & Lackner, 2012, and *E. unguiculatus* (Ross, 1939), are also provided.

Keywords

Eremosaprinus warneri, new species, Coleoptera, Histeridae, Saprininae, North America, inquiliny

Introduction

Shortly following the recently published revision of the obligate mammal burrowdwelling genus *Eremosaprinus* Ross, 1939 (Tishechkin and Lackner 2012), study of more recently collected *Eremosaprinus* specimens from Arizona revealed an additional undescribed species of this genus. In this paper we describe the species, update the identification key for the genus and list the new distributional information on several other *Eremosaprinus* species. We refer readers to Tishechkin and Lackner (2012) for methods, conventions and abbreviations (LSAM is the abbreviation used here for the Louisiana State Arthropod Museum). References to the figures from that publication are made below in **bold italic**. All specimens of described species listed below were collected by W. B. Warner, unless specified otherwise, and are deposited in CWBW.

Revised key to *Eremosaprinus* species (sensu Tishechkin and Lackner 2012)

The original key needs to be edited beginning with couplet 6. After studying a long series of the new species and revisiting the characters of *E. distinctus* Lundgren, 1992, *E. minutus* Tishechkin & Lackner, 2012, *E. rossi* Tishechkin & Lackner, 2012 and *E. verityi* Tishechkin & Lackner, 2012, we decided to drop from this couplet the mention of the dorsal microsculpture characters. The new species is very similar to *E. rossi* in overall appearance and has distinct background microsculpture, while in the only known *E. rossi* specimen it is almost nonexistent. We suspect, however, that the discovery of more *E. rossi* specimens might prove this species also possesses relatively distinct background microsculpture (as the new species does), the holotype appearing to be a somewhat worn specimen. So, to avoid possible confusion, we delete the mention of microsculpture characters from the key and use only unambiguous male characters. However, diagnosis of the so far unknown females of *E. rossi* might prove to be problematic without a reliable male association.

6 Males with pair of short, obtuse, triangular tubercles on posterior margin of metaventrite (*fig. 42*); protibia with at least three teeth on outer margins....7 Males without paired tubercles on posterior margin of metaventrite (fig. 112), but with two tubercles on basal end of abdominal setose patch (fig. 119); carinal prosternal striae widely separated, strongly concave; protibia with only two large teeth on outer margins...... E. rossi Tishechkin & Lackner, 2012 7 Fourth dorsal elytral striae anteriorly not connected with abbreviated sutural elytral striae; impression on metaventrites of males deep, circular; disc of 1st abdominal ventrite in males without a setose patch; carinal prosternal striae anteriorly united in semicircular loop (fig. 41)E. distinctus Lundgren, 1992 Fourth dorsal elytral striae anteriorly connected with complete sutural elytral striae under smooth arch; impression on metaventrites in males shallow, elongate or short triangular; disc of 1st abdominal ventrite in males medially with a

8 Impressions of metaventrite and 1st abdominal ventrite of males relatively small, occupying about half the lengths of metaventrite and 1st abdominal ventrite (occasionally up to two-thirds the length of 1st abdominal ventrite) (figs 92, 149); dorsal punctures small and sparse, especially on anterior part of elytral disc9 Males with wide and long setose impressions occupying entire length of metaventrite and 1st abdominal ventrite (Fig. 4); dorsal punctures large and dense throughout the surface (Fig. 1)......E. warneri sp. n. 9 Larger species, PEL: 2.70–3.60 mm; body dorsally entirely black; punctation of pygidium sparser, interspaces between punctures larger than punctures themselves; opaque microsculpture of pronotal and elytral discs sparse, inconspicuous; male genitalia (figs 157-165) compare with those in figs 100-108; known exclusively from California (Inyo and San Bernardino Counties)..... E. verityi Tishechkin & Lackner, 2012 Smaller species, PEL: 2.10-2.70 mm; body, especially pronotum dorsally paler, brownish; punctation of pygidium denser, punctures separated by approximately their diameter; opaque microsculpture of pronotal and elytral discs dense and conspicuous; male genitalia as on *figs 100–108*; known exclusively from Arizona (Cochise, Mohave, La Paz, Pima and Yuma Counties).....*E. minimus* Tishechkin & Lackner, 2012

Taxonomy

Eremosaprinus warneri sp. n.

http://zoobank.org/163E10DA-BBDF-4423-95FC-5C30F1B67D7F http://species-id.net/wiki/Eremosaprinus_warneri Figs 1–23



Figures 1–5. 1 *Eremosaprinus warneri* sp. n., habitus, dorsal view. **2** ditto, ventral view **3** ditto, lateral view **4** *Eremosaprinus warneri* sp. n., male, metaventrite + first abdominal ventrite **5** *Eremosaprinus warneri* sp. n., head, frontal view.

33 and 1 9 with the same locality, collector and collecting method, but collected on 9.x.-19.xi.2011.

Diagnosis. In general appearance, *E. warneri* has a close resemblance to the apparently sympatric *E. rossi*, both species possessing similar elytral strial patterns, dense dorsal punctation and a large elongate setose impression on the metaventrite and 1st abdominal ventrite in males. Furthermore, the two species share a synapomorphy of a microscopic slit-like aperture situated near the anterior margin of prosternum, just before the deep transverse sulcus across prosternal keel; this aperture can possibly be interpreted as a homology to the tiny foveae found in other congeners, which these species otherwise lack. The new species can be diagnosed by the presence of a pair of tubercles on the posterior margin of the male metaventrite in *E. warneri* (absent in *E. rossi*), the presence of a pair of tubercles on the posterior margin of the male 1st abdominal ventrite in *E. rossi* (absent in *E. warneri*) and the shape of the prosternal carinal striae (forming an almost circular loop in *E. rossi*, with a more elongate and narrow loop in *E. warneri*, compare Figs 9 and **112**).

Description. Body measurements: PEL: 2.4–3.3 mm; APW: 0.9–1.2 mm; PPW: 1.7–2.3 mm; EL: 1.5–2.1 mm; EW: 2.0–2.7 mm. Body (Figs 1–3) wide oval, convex, ventral surface flattened. Color dark brownish black, legs and antennae paler, antennal clubs dark rufous.

Antennae short, scape subquadrate, subequal to funicle in length; dorsal side with multiple long setae; pedicel enlarged, subquadrate. Antennal club (Fig. 7) small, spherical, slightly pointed apically, completely covered with short appressed tomentose sensilla intermingled with sparse short sub-erect sensilla. Antennal clubs ventrally with two rows of circular sensory areas situated above each other with three areas in each row; areas increased in size mediad; sensory areas dorsally likewise arranged in two rows, but areas of both dorsal rows approximately identical in size, circular; lower row contains five sensory areas while upper row contains three; sensory structures of antennal club (Fig. 6) in form of vesicles corresponding in number and shape to the sensory areas on the surface; no main vesicle "v" apparent.

Mouthparts: mandibles (Fig. 5) regularly rounded, with finely microsculptured surface and dense shallow punctures; mandibular apex acute and long, sub-apical tooth on left mandible small and obtuse. Labrum short, triangular, surface finely granulate; mentum (Fig. 8) subquadrate, anterior angles slightly produced, anterior margin medially with a tiny notch, surface around it with several setae; disc of mentum imbricate; lateral margins with a row of sparse ramose setae.

Frons (Fig. 5) moderately convex, with dense small anastomosing rugose punctures. Frontal stria absent; occipital stria complete, thin, carinate; supraorbital stria present along dorsal halves of inner margins of eyes, inconspicuous among rugose frontal punctation. Clypeus convex, lateral sides weakly so, anterior margin shallowly concave, its punctation slightly smaller that of frons.

Pronotum (Fig. 1) widest at base, lateral margins almost straight, anterior angles obtuse, narrowly rounded. Marginal pronotal stria poorly distinct among dense punctation laterally, completely absent behind head. Anterior margin of pronotum with a



Figure 6. *Eremosaprinus warneri* sp. n., left antennal club, dorsal view (white circles show sensory areas and corresponding vesicles of dorsal side, grey circles depict sensory areas and vesicles of ventral side).

fringe of tiny thin setae. Pronotal disc singly microsculptured, with moderate to large shallow dense punctures, interspaces between them smaller than punctures themselves, progressively becoming denser, somewhat larger and more elongate laterally, turning into fine longitudinal wrinkles in lateral thirds of pronotal width. Ante-scutellar depression indistinct; scutellum minute, triangular; pronotal hypomeron with background microsculpture and dense shallow longitudinally arranged punctures, with numerous short yellow setae.

Elytra (Fig. 1) with fine background micro-sculpture, completely covered with small to medium shallow, mostly elongate dense punctures, their interspaces approximately half as large as punctures themselves, but can be larger; being progressively larger and denser posteriorly and laterally, with a tendency to merge into shallow longitudinal wrinkles in elytral intervals and on posterior fourth. Elytral striae thin, finely punctuate, weakly costate. Outer subhumeral striae absent, humeral striae indistinct, mostly obscured by dense punctation, inner subhumeral striae complete, running from bases to near apices, but not attaining apex. First dorsal elytral striae almost complete, 2^{nd} to 4^{th} long, entering posterior fifth, sub-equal in lengths, 4^{th} dorsal elytral stria being usually somewhat shorter. No traces of 5^{th} dorsal elytral striae present, sutural ely-

tral striae complete, connected with 4th dorsal elytral striae under angulated wide arch, occasionally very narrowly interrupted anteriorly. Apical elytral striae absent; marginal elytral striae thin, slightly carinate, complete; marginal epipleural striae thin, distinct and complete. Elytral epipleura with punctation identical to lateral areas of elytra in dorsal parts, areas between marginal elytral and epipleural striae smooth and shiny, with few small punctures.

Propygidium narrow, with small shallow circular anostomosing punctures; pygidium long and moderately convex, with elongate anostomosing punctures similar to ones on posterior parts of elytra, progressively denser and wrinkle-like apically.

Anterior margin of median portion of prosternum (Fig. 9) straight, not elevated, marginal prosternal stria indistinct. Prosternal process laterally with dense small punctures in anterior third, dorsally with tiny scattered punctures, slightly convex. Carinal prosternal striae long, convergent between procoxae, thence moderately convex, approaching each other anteriorly, terminating freely next to microscopic slit-like aperture situated near anterior margin, just before deep transverse sulcus across prosternal keel (Fig. 9). Lateral prosternal striae absent. Carinal profile shallowly concave, with weak notch at transverse anterior sulcus.

Mesoventrite transverse, with small, shallow, moderately dense punctures throughout disc, anterior margin deeply concave. Marginal mesoventral stria thin, complete. Meso-metaventral sutural stria absent; meso-metaventral suture thin, distinct. Metaventrite long, with slightly larger punctures than those of mesoventrite. Metaventral profile weakly concave in males, slightly convex in females. Longitudinal suture of metaventrite distinct, complete, thin and impunctate. Most of discs of metaventrite and 1st abdominal sternite in males occupied by relatively deep elongate oval setose patch (Fig. 4). Setae of this patch flattened and dorso-ventrally appressed, cuticle mostly carpeted by setal cover; metaventral part with narrow weak keel along longitudinal suture. Lateral striae of metaventrite long, slightly abbreviated before metacoxa, punctuate, postmesocoxal striae represented by short outer fragment near anterior end of metepisternum. Lateral discs of metaventrite (Fig. 10) with large shallow dense (0.3–1.2), circular punctures; metepisternal discs with smaller denser punctures, becoming progressively sparser posteriorly. First abdominal ventrite of males mostly occupied by setose depression (Fig. 4), in females this setose depression absent, completely striate laterally; peripheral areas outside of depression with identical type of punctation as peripheral parts of disc of metaventrite.

All femora smooth and sparsely punctuate, wide; punctures of profemora slightly larger and denser than those of meso- and metafemora; profemora with a row of short stiff setae on both margins. Margins of meso- and metafemora with rows of shorter setae on dorsal sides, hidden from ventral aspect, an extra row of short stiff setae present on posterior margins.

Protibia (Fig. 11) rather wide, outer margins with four shallow teeth in anterior halves topped with small flattened denticles and with extra one or two tiny denticles toward bases. Anterior margins with one tiny denticle. Anterior surface of protibia with complete anterior protibial stria and with two complete rows of rather long sparse



Figures 7–14. 7 *Eremosaprinus warneri* sp. n., left antennal club, ventral view. 8 *Eremosaprinus warneri* sp. n., mentum, ventral view 9 *Eremosaprinus warneri* sp. n., prosternum 10 *Eremosaprinus warneri* sp. n., lateral disk of metaventrite + metepisternum 11 *Eremosaprinus warneri* sp. n., protibia, dorsal view 12 ditto, ventral view 13 *Eremosaprinus warneri* sp. n., mesotibia, dorsal view 14 *Eremosaprinus warneri* sp. n., metatibia, dorsal view.

setae. Protarsal groove deep; protibial spur tiny, inconspicuous. Posterior surfaces of protibia (Fig. 12) with outer portion irregularly rugosely punctate, clearly distinct from smooth narrow median portion, separated by irregular carinate elevation with a row of microscopic setae; posterior protibial stria complete, thin and carinate, on anterior half with a row of microscopic setae; setae of inner row double: one row of setae short and stiff; another row of setae approximately identical in length, but setae much thinner.

Mesotibia (Fig. 13) long and narrow, distinctly curved, outer margin with a row of tiny denticles and a row of long denticles, progressively increasing in size distally; setae of outer and median rows long and sparsely spaced. Anterior surfaces smooth, mesotibial spurs tiny and inconspicuous. Anterior and posterior mesotibial striae complete. Tibial apices with several relatively long thin denticles. Metatibia (Fig. 14) in all aspects similar to mesotibia, but slightly longer and thinner. All tarsi long and thin, meso- and metatarsomeres each with long (1.4–1.7 times corresponding tarsomere length) straight bristles ventrally and shorter, thinner bristle dorsally. First meso- and metatarsomeres with three ventral bristles, 2nd to 4th with a pair of such bristles, being uneven in length (outer ones distinctly shorter). Tarsal claws long, nearly straight, 0.5 times length of correspondent apical tarsomere.

Male genitalia: Eighth sternite entirely fused medially (Figs 15–16), medio-laterally with few pores, apically with rather large vela basally with two brushes of long, dense setae (most easily visible from lateral view, Fig. 19); two rows of shorter setae appear apically. Apices of 8th sternite with two small elongate membranous patches covered with microscopic setae. Apical part of 8th tergite medially faintly inwardly arcuate (Fig. 16); 8th tergite medio-laterally with pores. Eighth sternite and tergite fused laterally (Fig. 19). Ninth tergite (Fig. 20) laterally with few pores, apical margin almost straight, with a conspicuous median projection observable from ventral view (Fig. 21); 10th tergite basally inwardly arcuate. Spiculum gastrale (Figs 22–23) almost parallel-sided with dilated ends; apical end strongly sclerotized, with two horn-like projections; basal end of spiculum gastrale outwardly arcuate. Aedeagus (Figs 17–18) strongly sclerotized, almost parallel-sided on basal half, slightly thickened on apical half; convergent apically. Parameres fused on approximately basal third, aedeagus strongly curved ventrad (Fig. 18). Basal piece of aedeagus short, its ratio to parameres length approximately 1:4.

Remarks. Sensory structures of the antenna of *E. warneri* differ substantially from those of the type species of the genus, *E. unguiculatus* (Ross, 1939); compare Fig. 6 with that of Tishechkin and Lackner (2012: *fig. 138*). Such disparity between the species of *Eremosaprinus* was discussed previously (Tishechkin and Lackner 2012: 50) and the unity of the genus remains unclear. We prefer to keep this newly described species tentatively in the genus pending larger series of all already known species – something that would enable us to study sensory organs of the antennae among all species and allow us to reconstruct the phylogeny of the genus on species level.

Etymology. We dedicate this species to our colleague and friend Bill Warner, an enthusiastic student and collector of Arizona beetles, histerids in particular, who collected the entire type series of this species and many other *Eremosaprinus* specimens.



Figures 15–23. 15 *Eremosaprinus warneri* sp. n., 8th sternite and tergite, ventral view. 16 ditto, dorsal view 17 *Eremosaprinus warneri* sp. n., aedeagus, dorsal view 18 ditto, lateral view 19 *Eremosaprinus warneri* sp. n., 8th sternite and tergite, lateral view 20 *Eremosaprinus warneri* sp. n., 9th + 10th tergites, dorsal view 21 ditto, lateral view 22 *Eremosaprinus warneri* sp. n., spiculum gastrale, ventral view 23 ditto, lateral view.

Biology. According to the collector, W.B. Warner, the type series of this species was collected using barrier and black pitfall traps that were set around banner-tail kangaroo rat (*Dipodomys spectabilis* Merriam, 1890) burrows (mostly within 100 cm radius of the burrow entrances). The new species is most likely an inquiline inhabiting the burrows of the above-mentioned rodent (W.B. Warner, pers. comm).

Distribution. USA, Arizona.

New data on the distribution of Eremosaprinus species

Eremosaprinus hubbardi (Wenzel, 1939)

Material studied. 1 specimen: Arizona, La Paz Co., dunes 11 mi S Ehrenberg, 33°28'03"N, 114°36'26"W, 12.ii.-4.iii.2012; 6 specimens: Arizona, Maricopa Co., nr. Agua Caliente, 32°57'00"N, 113°17'31"W, 11.ii.–25.iii.2012; 11 specimens: Arizona, Yuma Co., SW of Dateland, 32°47'25"N, 113°32'54"W, 11.ii.–25.iii.2012; 1 specimen: Arizona, Yuma Co., 6 mi. N Gila Rd. on Hwy. 95, 32°50'23"N, 114°22'07"W, 12.ii.-4.iii.2012; 2 specimens: California, Riverside Co., Wiley Well Rest Stop on I-10, 33°36'18"N, 114°54'15"W, 18.ii.–4.iii.2012; 14 specimens: California, San Bernardino Co., Rt. 62, 12 mi ENE junction with Rt. 177, J. Saulnier, 30.xi.–22.xii.2011. First records for La Paz and Maricopa Counties, Arizona.

Eremosaprinus distinctus Lundgren, 1992

Material studied. 1 specimen: California, San Bernardino Co., Rt. 62, 12 mi ENE junction with Rt. 177, J. Saulnier, 30.xi.-22.xii.2011. First record from San Bernardino Co., California.

Eremosaprinus minimus Tishechkin & Lackner, 2012

Material studied. 40 specimens: Arizona, Cochise Co., Bagby Rd., 0.2 mi W Central Hwy., 31°33'14"N, 109°42'06"W, 28.viii.2011-10.vi.2012; 31 specimens: Arizona, Cochise Co., Birch Rd., 4.1 mi E Hwy. 191, 31°58'43"N, 109°46'41"W, 28.viii.2011-10.vi.2012; 2 specimens: Arizona, Cochise Co., 1.5mi.S jct.Hwys.191 and 181, 31°51'44"N, 109°41'59"W, 9.x.-19.xi.2011; 1 specimens: Arizona, Cochise Co., 3 mi.S Wilcox, C. W. O'Brien, 16.i.2008; 1 specimen: Arizona, La Paz Co., Ave. 51E, 0.5mi S of I-10, 33°37'27"N, 113°45'58"W, 12.ii.-4.iii.2012; 2 specimens: Arizona, Yuma Co., SW of Dateland, 32°47'25"N113°32'54"W, 11.ii.-25.iii.2012. First record for La Paz Co., Arizona.

Eremosaprinus unguiculatus (Ross, 1939)

Material studied. 7 specimens: Arizona, La Paz Co., dunes 11 mi S Ehrenberg, 33°28'03"N, 114°36'26"W, 12.ii.–4.iii.2012; 57 specimens: Arizona, Maricopa Co., nr. Agua Caliente, 32°57'00"N, 113°17'31"W, 11.ii.–25.iii.2012; 1 specimen: California, Riverside Co., Wiley Well Rest Stop on I-10, 33°36'18"N, 114°54'15"W, 18.ii.-4.iii.2012. First records for La Paz and Maricopa Co., Arizona.

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RESEARCH ARTICLE



The South American radiation of Jerrybuccinum (Gastropoda, Buccinidae), with a new deep-water species from Chile

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Abstract

A new deep water species from off the Chilean coast, *Jerrybuccinum kantori* **sp. n.**, is described. The animal is equipped with a large statocyst. *Kryptos explorator* Fraussen & Sellanes, 2008 from off Concepción is found to be congeneric and transferred to the genus *Jerrybuccinum*. Differences in size and sculpture serve to distinguish the new species from *J. explorator*. Both Chilean species are associated with methane seep or low oxygen environments. They are compared with *J. malvinense* Kantor & Pastorino, 2009 and two still unnamed species from the Falkland Plateau.

Keywords

New taxa, East Pacific, methane seep, low oxygen environments

Introduction

The Patagonian marine environments of the SW Atlantic host a vast marine fauna with high pelagic and benthic biomass. The benthic molluscan fauna has been proven to be rich in endemic species and genera. Recent investigations have resulted in the descriptions of a number of genera that are typical of the Patagonian continental slope fauna (e.g. Harasewych et al. 2000, Kantor and Pastorino 2009, Harasewych and Pastorino 2010). The fauna off southern Chile, the Pacific Ocean counterpart of the Patagonian region, is still mostly underestimated by malacologists even though a number of endemic species have recently been described (Fraussen and Hadorn 2000, Holmes et al. 2005, Oliver and Sellanes 2005, Sellanes and Krylova 2005, Houart and Sellanes 2006, Vilvens and Sellanes 2006, Fraussen and Sellanes 2007, Fraussen et al. 2012, Araya 2013, Krylova et al. 2014). For a brief overview of past scientific expeditions that produced noteworthy malacological contributions we refer to Fraussen et al. (2008).

The goals of the present paper are to contribute to the knowledge of the family Buccinidae from north to south-central Chile, comparing species with their SW Atlantic counterparts, and to continue the effort of describing the malacofauna, whether endemic or not, of Chilean methane seeps.

The Concepción Methane Seep Area (CMSA; ~37°S; ~800 m water depth) has been the source of many new species of molluscs in the previous decade. We herein add a new species of gastropod, inhabiting both the CMSA and a shallower water area located northwards. The new area is situated within the lower boundary of the SE Pacific permanent oxygen minimum zone (OMZ; Wyrtki 1962). At this place, the presence of chemosymbiotic bivalves (including a new genus of vesicomyid clam; Krylova et al. 2014), and tubeworms typical of seep communities may indicate the existence of a methane seep habitat, or at least a reducing habitat associated to the OMZ, but further thorough studies are needed to prove this thesis. This area has been named El Quisco Seep Site (after the adjacent coastal town) and it is located at about 350 m depth at approximately 33°S.

The new species is compared with its two congeneric species known so far, one from the Atlantic and one from the Pacific, as well as with two still undescribed species from the Patagonian shelf.

Materials and methods

The material of the new species described in this paper was collected during the following cruises: AIW (R/V Vidal Gormáz), ONR (R/V Vidal Gormáz) and INSPIRE (R/V Melville).

For radula preparation the body of paratype 1 was extracted from the shell and dissected to isolate the buccal complex. It was treated with a 1% solution of sodium hypochlorite until the soft tissue was completely dissolved. Subsequently, the radula was cleaned in several shifts of distilled water, unfolded and mounted for SEM examination.

Abbreviations

AGT	Agassiz trawl
CBUCN	Colecciones Biológicas Universidad Católica del Norte, Coquimbo, Chile
CMSA	Concepción Methane Seep Area
EQSS	El Quisco Seep Site
KBIN	Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium
KF	collection of Koen Fraussen, Belgium
MNHN	Muséum national d'Histoire naturelle, Paris, France
MNHNCL	Museo Nacional de Historia Natural, Santiago, Chile
PS	collection of Peter Stahlschmidt, Germany
lv	live collected specimen
dd	empty shell

Results

Systematics

Class Gastropoda Cuvier, 1797 Order Neogastropoda Wenz, 1938 Superfamily Buccinoidea Rafinesque, 1815 Family Buccinidae Rafinesque, 1815

Genus Jerrybuccinum Kantor & Pastorino, 2009 http://species-id.net/wiki/Jerrybuccinum

Type species. *Jerrybuccinum malvinense* Kantor & Pastorino, 2009 (type locality: Falkland Islands (Islas Malvinas), 52°00'S; 56°36'W, R/V Eltanin cruise 7 st 558, 384–494 m).

Diagnosis. Jerrybuccinum is characterised by a slender, fusiform shell with a high spire but a moderately long siphonal canal, a broad but blunt protoconch ornamented with fine spiral cords, a sculpture consisting of rather short, slightly bended axial ribs on the adapical part of the whorls and two or more accentuated spiral cords at the transition to the base. In most species (*J. malvinense*, the type species, *J. explorator* and *J.* species 1) the spiral cord delimitating the base forms a strong keel. This characteristic is subject to variation within the genus as the keel may be replaced by one or more weaker but slightly broader spiral cords (*J. kantori* sp. n. and *J.* species 2).

The radula is characterised by a rectangular central tooth with slightly curved base and with one (Kantor and Pastorino 2009) or two (present paper) small cusps and tricuspid lateral teeth with a long basal projection at the outer side.

Kryptos Jeffreys in Dautzenberg and Fischer 1896 (type species *Kryptos elegans*, Jeffreys in Dautzenberg and Fischer 1896 = *Pleurotomella koehleri* Locard, 1896) dif-

fers by the presence of axial sculpture on the protoconch (rather than only fine spiral cords), a broad interspace situated between the spiral cords along the periphery (rather than a spiral keel), carinated whorls (type species) or sculptured with sharp keels along the periphery (*K. tholoides* (Watson, 1882)), an operculum with terminal nucleus (rather than just falling within the margin) and a radula with a rectangular middle tooth without prominent cusps (Bouchet and Warén 1985: fig. 487). Bouchet and Warén (1985: 196) noted that *K. koehleri* lacks eyes.

Americominella Klappenbach & Ureta, 1972 (type species: *Americominella duartei* Klappenbach & Ureta, 1972, a senior synonym of *Americominella longisetosus* (Castellanos & Fernandez, 1972)) (= *Echinosipho* Kaiser, 1977, type species: *Echinosipho aculeatum* Kaiser, 1977 a senior synonym of *A. duartei*) from the Patagonian continental shelf is somewhat similar in protoconch morphology but differs by the radula, which has a clearly tricuspid central tooth with longer cusps and a broader base.

Buccipagoda Ponder, 2010 (type species: *Kapala kengrahami* Ponder, 1982) from Australia has a radula with an identical central tooth, but which differs by the lateral teeth with one large outer cusp and more than 5 small inner cusps.

Antarctoneptunea Dell, 1972 (type species: Fusitriton aurora Hedley, 1916) from off Antarctica is similar in shape but differs in the absence of axial sculpture, in having a large papilliform protoconch, a radula with a tricuspid central tooth and a much larger adult size.

Prosipho Thiele, 1912 (type species: *Prosipho gaussianus* Thiele, 1912) is a rather heterogeneous group (Engl 2012) mainly living near Antarctica, with slender shells ornamented with a dominant spiral sculpture. Some *Jerrybuccinum*, especially the smaller species without obvious axial sculpture like *J*. species 2, may be confused with them. *Prosipho* differs by the smaller protoconch with smooth whorls, the axial sculpture that is usually absent or consisting of fine and sharp minute ridges that are straight (rather than broad and inclined ribs) and different radula morphology.

Included species.

Jerrybuccinum malvinense Kantor & Pastorino, 2009 (Falkland Plateau), type species; *Jerrybuccinum explorator* new combination (Fraussen and Sellanes 2008) (Chile); *Jerrybuccinum kantori* new species (Chile); *Jerrybuccinum* species 1 (Falkland Plateau);

Jerrybuccinum species 2 (Falkland Plateau).

Jerrybuccinum malvinense Kantor & Pastorino, 2009

http://species-id.net/wiki/Jerrybuccinum_malvinense Figures 15–16, 27

Jerrybuccinum malvinense Kantor & Pastorino, 2009: 49-52, figs 1-12.

Type material. Holotype in USNM-887765. Paratype in USNM-898774.

Type locality. Falkland Islands (Islas Malvinas), 52°00'S, 56°36'W, R/V ELTA-NIN, cruise 7, sta. 558, 14 Mar. 1963, 646–845 m.

Remarks. The single shell that we studied is a slightly eroded and damaged empty shell collected off the Falkland Islands, but without exact locality data.

Jerrybuccinum species 1

Figures 17–18

Remarks. The single shell that we studied is a damaged empty shell collected off the Falkland Islands. This species differs from *J. malvinense* by the broader shape, the bigger protoconch, the narrower axial ribs with broader interspaces, the finer spiral cords on the base and the larger size even though it is a subadult shell.

Jerrybuccinum species 2

Figures 19–20

Remarks. The single shell that we studied was collected north of the Falkland Islands. This species is characterised by having a weak axial sculpture consisting of narrow axial ribs on the spire whorls and a smooth body whorl; the absence of the spiral keel that delimits the shell base of typical *Jerrybuccinum*, but the presence of two slightly broader spiral cords. The protoconch is ornamented with fine spiral cords, a feature that is typical of the genus.

Jerrybuccinum explorator (Fraussen & Sellanes, 2008), comb. n.

http://species-id.net/wiki/Jerrybuccinum_explorator Figures 12–14, 26

Kryptos explorator Fraussen & Sellanes, 2008: 102-104, figs 5-6, 16-25.

Type material. Holotype in MNHNCL-5866, two paratypes in MNHN-CL-5867-5868, two paratypes in KF-5180-5181 and a paratype in MNHN-9961.

Type locality. South-central Chile, R/V Vidal Gormáz (SeepOx Cruise, AGT 6-7, 09/02/2006), CMSA, northwest of the Bay of Concepción, 36°20'97S; 73°44'86W, 850 m.

Remarks. This species was tentatively placed in the genus *Kryptos* (Fraussen and Sellanes 2008) based on similarities in sculpture and radula and to prevent the description of a monotypic genus. The radula is identical to the radula of *J. malvinense*. It is characterised by a monocuspid central tooth with quadrangular base and by tricuspid lateral teeth that have a broad base prolonged with a basal projection. The shape, the axial and spiral sculpture of the shell and the shape of the operculum are similar. We hereby assign this species to *Jerrybuccinum*.

Jerrybuccinum kantori sp. n.

http://zoobank.org/BCD550A7-F2E1-4584-93A9-8BAAA3E84665 http://species-id.net/wiki/Jerrybuccinum_kantori Figures 1–11, 21–25

Type material. Holotype (MNHNCL-7589) (14.5 mm), Chile, northwest of the Bay of Concepción, R/V Melville, INSPIRE cruise, AGT 04, 36°23.595'S, 73°42.910'W, ~700 m deep, March 10, 2010, lv.

Paratype 1 (KF-5441) (12.1 mm), same locality as holotype, lv.

Paratype 2 (MNHNCL-7590) (15.7 mm), Chile, northwest of the Bay of Concepción, R/V Vidal Gormáz, ONR cruise, AGT 3.4, 36°10'S; 73°34'W, 521–613 m deep, October 2004, lv.

Paratypes 3-4 (KF-7019-7020) (13.6-11.6 mm), same locality as paratype 2, lv.

Paratypes 5–6 (MNHNCL-7591) (13.0–13.2 mm), Chile, northwest of the Bay of Concepción, R/V Vidal Gormáz, AIW cruise, 36°24.12'S, 73°36.44'W, 606 m deep, December 2003, lv.

Paratypes 7–8 (PS-150148) (12.5–10.5 mm) Chile, off El Quisco, R/V Melville, INSPIRE cruise, AGT 10, 33°23.378'S, 71°52.782'W, -340 m deep, March 14, 2010, lv.

Paratype 9 (MNHNCL-7592) (9.5 mm), same locality as paratypes 7–8.

Paratype 10 (KF-5440) (8.8 mm), same locality as paratypes 7–8.

Paratypes 11–13 (CBUCN-003284) (8.1, 8.0, 6.2 mm juveniles), same locality as paratypes 7–8.

Type locality. Chile, northwest of the Bay of Concepción, 36°23.595'S; 73°42.910'W, -700 m deep.

Material examined. Apart from the type material listed above 20 additional specimens (6.3–11.3 mm; 19 lv, 1 dd; JS) collected together with the paratypes 7 and 8 were studied.

Range and habitat: Only known from the type material and the specimens from off Concepción and off El Quisco. Most of the specimens of *J. kantori* sp. n. collected so far were associated with fauna typical of methane seeps (vesicomyid, solemyid, lucinid, and thyasirid bivalves). However, the scarce knowledge of the bathyal SE Pacific malacofauna still keeps us from establishing this species as an obligatory dweller of seep environments or other reducing habitats.

Description. Shell small for genus (up to 15.7 mm), thin but solid, semi-transparent, off-white. Shape broadly fusiform with high spire and moderately short siphonal canal.

Apex and protoconch eroded in all studied specimens. Remaining teleoconch whorls 6 (holotype) or 7 (paratype 3) in number, convex, adapical part slightly flattened, thereby accentuating a rather carinated shape. Suture distinct.

Upper teleoconch whorls with 5 or 6 fine spiral cords of unequal strength, separated by deep interspaces of equal width; slightly increasing in number. Penultimate whorl with 8–11 spiral cords, adapical spiral cords fine, abapical spiral cords slightly broader, interspaces of equal size or twice as wide. Body whorl with 21 or 22 fine spiral cords of unequal strength; 9 or 10 adapical spiral cords fine with moderately



Figures 1–11. Jerrybuccinum kantori sp. n. 1–4 Holotype, 14.5 mm, Chile, northwest of the Bay of Concepción, R/V Melville, INSPIRE cruise, AGT 04, 36°23.595'S, 73°42.910'W, -700 m, MNHNCL-7589 **5** Paratype 7, 12.5 mm, Chile, off El Quisco, R/V Melville, INSPIRE cruise, AGT 10, 33°23.378'S, 71°52.782'W, -340 m, PS-150148 **6–7** paratype 9, 9.5 mm, same locality as paratype 7, MNHNCL-7592 **8–9** operculum of paratype 6, 4.2 mm 10–11 operculum of paratype 9, 2.5 mm 12–14 Jerrybuccinum explorator (Fraussen & Sellanes, 2008) 12–13 Paratype 3, 28.9 mm, Chile, off Concepción, 36°22'68 S, 73°42'46 W, 708–709 m, KF-5180 14 Operculum of holotype, 6.6 mm, Chile, northwest of the Bay of Concepción, 36°20'97 S, 73°44'86 W, 850 m, MNHNCL-5866 15–16 Jerrybuccinum malvinense Kantor & Pastorino, 2009 1, 19.6 mm, Falkland Plateau, 700 m, KF-1989 17–18 Jerrybuccinum species 1, 34.4 mm, Falkland Plateau, 700 m, KF-1609 19–20 Jerrybuccinum species 2, 18.2 mm, north off Falkland Islands, 51° S, 60° W, 850–900 m, KF-1763.



Figures 21–27. *Jerrybuccinum kantori* sp. n. **21–24** radula of paratype 1, scalebar: 10 micrometer **25** statocyst of paratype 1, scalebar: 100 micrometer **26** radula of *Jerrybuccinum explorator*, scalebar: 100 micrometer. **27** radula of *Jerrybuccinum malvinense*, scalebar: 100 micrometer, after Kantor & Pastorino, 2009: fig. 11.

narrow interspaces; 2 or 3 interspaces situated along transition from whorl to base much broader; interspaces on base of unequal strength. Subadult shells with 2 more pronounced spiral cords visible. Siphonal canal with about 9 broad, flattened spiral cords separated by narrow interspaces.

Upper teleoconch whorls with 10 or 11 moderately narrow but pronounced, weakly bended axial ribs, slightly weaker near both sutures. Badly eroded ribs party or entirely decollate, forming a deep depression with sharp margins. Penultimate whorl with 13–16 weaker ribs on adapical half of body whorl. Base and upper border of subsutural slope smooth. Body whorl of adult specimens almost smooth. All whorls covered with fine, weakly curved incremental lines.

Aperture round; columella concave, smooth; callus thin, glossy. Outer lip thin, moderately sharp, laterally curved following the shape of the incremental lines. Siphonal canal narrow, rather short, open.

Operculum corneous, thin, elongate, concentric, nucleus situated near lower margin, almost terminal, forming a sharp tip. Colour pale brownish, with a slightly darker pattern forming a V-shaped mark that grows from the nucleus (Figs 8–11), juveniles with a thinner, more translucent operculum (Figs 10–11).

Periostracum greyish with a greenish shine, thin, smooth, well-adherent.

Radula (Figs 21–24) typical of genus: central tooth rather rectangular with concave base and 3, occasionally 1, short cusps; lateral teeth tricuspid with large outer cusp and small middle cusp.

Animal with a moderately large statocyst (Fig. 25), measuring more than 150 micrometres in diameter, found after dissolving the animal during radula preparation.

Comparison. *Jerrybuccinum kantori* new species is characterised by having a moderately broad shape, a weakly carinated shape of the teleoconch whorls, axial ribs that are moderately broad and quite straight when compared to the other species of the genus and a small adult size.

Jerrybuccinum explorator from Chile differs by the more slender shape with higher spire, the more convex whorls, the numerous and narrower axial ribs that are also more twisted, the numerous and finer spiral cords, the browner periostracum and the larger adult size.

Jerrybuccinum malvinense (the type species of the genus) differs by the more slender shape with higher spire, the more convex whorls, the presence of an obvious, pronounced spiral cord ranging from whorl to base at the transition and the larger adult size.

Etymology. Jerrybuccinum kantori new species is named to honour Yuri Kantor for his numerous important contributions to malacology.

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RESEARCH ARTICLE



A new Liopropoma sea bass (Serranidae, Epinephelinae, Liopropomini) from deep reefs off Curaçao, southern Caribbean, with comments on depth distributions of western Atlantic liopropomins

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Abstract

Collecting reef-fish specimens using a manned submersible diving to 300 m off Curaçao, southern Caribbean, is resulting in the discovery of numerous new fish species. The new *Liopropoma* sea bass described here differs from other western Atlantic members of the genus in having VIII, 13 dorsal-fin rays; a moderately indented dorsal-fin margin; a yellow-orange stripe along the entire upper lip; a series of approximately 13 white, chevron-shaped markings on the ventral portion of the trunk; and a reddish-black blotch on the tip of the lower caudal-fin lobe. The new species, with predominantly yellow body and fins, closely resembles the other two "golden basses" found together with it at Curaçao: *L. aberrans* and *L. olneyi*. It also shares morphological features with the other western Atlantic liopropomin genus, *Bathyanthias*, are monophyletic with respect to Indo-Pacific *Liopropoma*, and that *Bathyanthias* is nested within *Liopropoma*, indicating a need for further study of the generic limits of *Liopropoma*. The phylogenetic data also suggest that western Atlantic liopropoma. The phylogenetic data also suggest that western Atlantic liopropoma the also shares that different depth maxima (3–135 m, 30–150 m, 133–411 m). The new species has the deepest depth range (182–241 m) of any known western Atlantic *Liopropoma* species. Both allopatric and depth-mediated ecological speciation may have contributed to the evolution of western Atlantic Liopropomini.

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Keywords

Liopropoma aberrans, Liopropoma olneyi, submersible, Substation Curaçao, Deep Reef Observation Project (DROP), DNA barcoding, phylogeny, modes of speciation

Introduction

Submersible diving to 300 m off Curaçao in the southern Caribbean as part of the Smithsonian Institution's Deep Reef Observation Project (DROP) is expanding our knowledge of the deep-reef Caribbean fish fauna (Baldwin and Robertson 2013, Baldwin and Johnson 2014). Recent collections of fishes included multiple individuals of what we initially identified as *Liopropoma aberrans* (Poey 1860) based on their predominantly golden color pattern. Subsequent analysis of mitochondrial DNA sequences (COI) from those specimens, detailed morphological examination of the preserved voucher specimens, and the discovery of consistent patterns of variation in coloration in photographs of vouchers taken prior to preservation led to the description of some of those individuals as a new species, *L. olneyi* Baldwin & Johnson, 2014. Additional genetic and morphological data indicate that the "golden basses" off Curaçao, in fact, comprise three species, *L. olneyi*, plus one undescribed species. Herein we describe this third species, *Liopropoma santi* sp. n.

Liopropoma (Atlantic and Pacific), *Bathyanthias* (western Atlantic), and the monotypic *Rainfordia* (Indo-Pacific) form the monophyletic epinepheline serranid tribe Liopropomini (Baldwin and Johnson 1993). Twelve species of liopropomins currently are known from the western Atlantic, including the new species described herein: seven species of *Liopropoma*, four species of *Bathyanthias*, and a putative new species of the latter genus that we refer to here. These western Atlantic liopropomin species inhabit both shallow (< 50 m) and deep (to 411 m) reefs in Caribbean and adjacent waters. To compare species depth preferences, we use the known depth maximum and minimum for each species. To investigate how deep and shallow species are interrelated, we use the COI data to hypothesize the phylogeny of the group and then analyze the results in the context of the known depth distributions of the various species. Based on these results, we comment on possible modes of speciation in western Atlantic liopropomins.

Materials and methods

The manned submersible *Curasub* (http://www.substation-Curacao.com) was employed to collect fishes and invertebrates during various field periods between 2011 and 2013. Fish specimens were collected using the fish anesthetic quinaldine pumped from a reservoir through a tube attached to one hydraulic arm of the sub and a suction hose (that uses the same pump as the anesthetic-delivery apparatus) attached to the other arm. The latter empties into a vented plexiglass cylinder attached to the outside of the sub. At the surface, the specimens were measured, photographed, tissue sampled (muscle
biopsy from right side) and preserved. They were later x-rayed with a digital radiography system. Counts and measurements included in the description follow Hubbs and Lagler (1958) and Randall and Taylor (1988). Measurements were made to the nearest 0.1 mm with an ocular micrometer fitted into a Wild stereomicroscope (smallest specimen) or with needle-point dial calipers. Institutional abbreviations follow Sabaj Pérez (2012).

Tissue samples for DNA Barcoding were stored in saturated salt-DMSO (dimethyl sulfoxide) buffer (Seutin et al. 1991). DNA extraction, PCR, sequencing cytochrome c oxidase subunit I (COI), and editing COI sequences were performed as outlined by Weigt et al. (2012). A neighbor-joining tree (Saitou and Nei 1987) was generated using PAUP*4.1 (Swofford 2002) on an analysis of Kimura two-parameter distances (Kimura 1980). The neighbor-joining tree shows genetic distances in COI among individuals and how they cluster into genetically distinct lineages, which, in teleost fishes, correspond well with species (e.g. Baldwin and Weigt 2012, Weigt et al. 2012). Interspecific phylogenetic relationships were hypothesized for western Atlantic liopropomins and three Indo-Pacific species of Liopropoma based on maximum parsimony analysis of the COI sequences using heuristic searches in PAUP*4.1. Characters were equally weighted and left unordered. The resulting equally parsimonious trees were summarized using the strict consensus method. Outgroups for both analyses were two members of the sister group of the Liopropomini - Grammistes sexlineatus (Thunberg, 1782) and Rypticus carpenteri Baldwin & Weigt, 2012, of the tribe Grammistini (Baldwin and Johnson 1993), and the trees were rooted on a more distant outgroup, Scorpaena plumieri of the family Scorpaenidae. We follow Johnson (1983) and Baldwin and Johnson (1993) in recognizing a monophyletic family Serranidae and subfamily Epinephelinae pending resolution of serranid relationships in light of conflicting hypotheses based on molecular data (e.g., Smith and Craig 2007, Betancur et al. 2013, Near et al. 2013).

The label for each entry on the neighbor-joining tree is an assigned DNA number, and we include that number in the designation of type specimens and in some figure captions. Abbreviations used in DNA numbers are as follows: BAH–Bahamas, BLZ–Belize, CUR–Curacao, FLST–Florida Straits, FWRI–Florida Wildlife Research Institute, MBIO–Moorea Biocode Project, MCgroup–Matthew Craig, MOC–*Miguel Oliver* Caribbean Cruise, MOOP–Moorea Deep Reef, TOB–Tobago. GenSeq nomenclature for DNA sequences (Chakrabarty et al. 2013) and GenBank information are presented along with museum catalog numbers for voucher specimens in the Appendix.

Results

The neighbor-joining tree (Fig. 1) shows how individual specimens of western Atlantic *Liopropoma* sort into genetic lineages based on similarity in COI sequences. Lineages correlate well with currently recognized species. Genetic distance in COI between pairs of species of western Atlantic *Liopropoma* ranges from 5–18%, and distance between *L. santi* sp. n., and other western Atlantic *Liopropoma* species is 13–18% (Table 1). Average intraspecific variation for western Atlantic *Liopropoma* is 0–0.3%, 0.2% for *L. santi*.



0.03

Figure 1. Neighbor-joining tree derived from COI sequences for western Atlantic *Liopropoma*, the Indo-Pacific *L. lunulatum*, and related taxa. The tree was rooted on *Scorpaena plumieri*. Divergence represented by scale bar = 3%. Photographs of *L. rubre* and *L. mowbrayi* by James Van Tassell and Ross Robertson.

Liopropoma santi sp. n.

http://zoobank.org/83D20375-39CA-457D-8D54-127ACC3ED0B7 http://species-id.net/wiki/Liopropoma_santi Figs 2–4, Spot-tail Golden Bass

Type locality. Curaçao, southern Caribbean

Holotype. USNM 426811, 116 mm SL, DNA #CUR 13253, *Curasub* submersible, sta. 13-14, southern Caribbean, Curaçao, off Substation Curaçao downline, near 12°05.069'N, 68°53.886'W, 241 m, quinaldine, 9 Aug 2013, C. C. Baldwin, D. R. Robertson, A. Driskell, B. van Bebber.

Paratypes. USNM 426813, 76.2 mm SL, DNA #CUR 13280, *Curasub* submersible, sta. 13–19, southern Caribbean, Curaçao, Playa Forti, Westpoint, 12°22.001'N, 69°9.005 W, 182 m, quinaldine, 15 Aug 2013, A. Schrier, N. Knowlton, R. Sant, B. van Bebber. USNM 414824, 42.0 mm SL, DNA #CUR 12314, *Curasub* submersible, sta. 12–19,

Table 1. Average (and range) Kimura two-parameter distance summary for species of western Atlantic *Liopropoma* (7), Indo-Pacific *Liopropoma* (1), western Atlantic *Bathyanthias* (2), and outgroups *Grammistes, Rypticus*, and *Scorpaena* based on cytochrome c oxidase I (COI) sequences of individuals represented in the neighbor-joining tree in Figure 1. Intraspecific averages are shown in bold. "na" = not applicable (n=1).

	L. aberrans	L. carmabi	L. eukrines	L. lunulatum
	W. Atl.	W. Atl.	W. Atl.	Indo–Pacific
	(n=6)	(n=9)	(n=1)	(n=2)
L. aberrans	0.3 (0-0.6)			
L. carmabi	14.6 (14.2–15.2)	0.2 (0-0.6)		
L. eukrines	10.5 (10.2–10.8)	15.1 (14.8–15.6)	na	
L. lunulatum	14.8 (14.6–15.1)	16.4 (16.1–16.9)	14 (14.0–14.1)	0.1 (0-0.2)
L. mowbrayi	12.2 (11.9–12.5)	8.6 (8.2–9.1)	13.5 (13.4–13.9)	15.5 (15.3–15.8)
L. olneyi	11.8 (11.5–12.1)	13.6 (13.4–14.2)	13 (12.8–13.1)	14.7 (14.4–14.9)
L. rubre	11.9 (11.5–12.4)	10.5 (10.1–10.9)	12.9 (12.8–13.3)	15.8 (15.3–16)
L. santi sp. n.	16.2 (16.0–16.7)	17.6 (17.1–18.4)	15.2 (15.0–15.6)	16.4 (16.0–16.9)
B. mexicanus	16.1 (15.8–16.4)	17.6 (17.1–18.4)	15.2 (15.0–15.6)	16.4 (16.0–16.9)
Bathyanthias sp	16.8 (16.5–17)	15.4 (15.2–15.7)	15.4 (-)	16 (15.9–16.1)
G. sexlineatus	18.6 (18.3–18.8)	17.9 (17.7–18.4)	18 (-)	17 (16.9–17.1)
R. carpenteri	17.3 (17.1–17.5)	17.9 (17.9–18.1)	14.8 (-)	15.4 (15.4–15.5)
S. plumieri	21.4 (21.2–21.5)	21.6 (21.4–22)	20.9 (-)	19.8 (19.7–19.8)

	L. mowbrayi	L. olneyi	L. rubre	L. santi sp. n.
	W. Atl.	W. Atl.	W. Atl.	W. Atl.
	(n=9)	(n=9)	(n=12)	(n=3)
L. mowbrayi	0.2 (0-0.6)			
L. olneyi	13.3 (13.0–13.7)	0 (0-0.3)		
L. rubre	5.7 (5.3-6.0)	12.5 (12.2–13.2)	0 (0-0.3)	
L. santi sp. n.	15.5 (14.8–16.5)	13.3 (13.0–13.5)	16.4 (15.9–17.6)	0.2 (0.0-0.3)
B. mexicanus	13.9 (13.8–14.1)	13.4 (13.4–13.5)	13.8 (13.7–14.3)	16.2 (15.9–16.9)
Bathyanthias sp	14.8 (14.6–14.9)	15.2 (15.1–15.4)	14.6 (14.5–14.8)	16.4 (16.2–16.7)
G. sexlineatus	18.1 (18.0–18.5)	18.9 (18.7–18.9)	18 (17.8–18.3)	20.8 (20.5–21.5)
R. carpenteri	16.8 (16.6–17)	18.6 (18.4–18.6)	17.4 (17.2–17.5)	17.5 (17.5–17.6)
S. plumieri	19.7 (19.5–20.4)	20.8 (20.8)	20.3 (20.2–20.6)	24.5 (24.4–24.8)

	B. mexicanus	Bathyanthias sp	G. sexlineatus	R. carpenteri	S. plumieri
	W. Atl.	W. Atl.	Indo-Pacific	W. Atl.	W. Atl.
	(n=1)	(n=1)	(n=1)	(n=1)	(n=1)
B. mexicanus	na				
<i>Bathyanthias</i> sp	13.7 (-)	na			
G. sexlineatus	19.8 (-)	15.9 (-)	na		
R. carpenteri	18.9 (-)	16.8 (-)	13.2 (-)	na	
S. plumieri	19.2 (-)	20.7 (-)	19.5 (-)	19.6 (–)	na

southern Caribbean, Curaçao, east of Substation Curaçao downline, near 12°05.069'N, 68°53.886'W, 209 m, 15 Aug 2012, C. C. Baldwin, B. Brandt, B. van Bebber.

Diagnosis. A liopropomin serranid with the following combination of characters: dorsal fin VIII,13; anal fin III, 8; pectoral fin 15; total gill rakers on first arch (including rudiments) 20–21; lateral-line scales 47–48; length of first dorsal spine 2.9–4.2% SL; margin of spinous dorsal fin moderately indented posteriorly in adults (fourth spine 11–12% SL, fifth and sixth spines only slightly shorter than fourth—6.9–10% SL); depth at origin of dorsal fin 23–26% SL; least depth of caudal peduncle 11–13% SL; orbit diameter 9.4–12% SL; yellow-orange stripe externally on upper lip; series of approximately 13 white, chevron-shaped markings on ventral portion of trunk; reddish-black blotch on distal portion of lower caudal-fin lobe; inhabiting depths of 182–241 m.

Description. Counts and measurements of holotype, if different from those of paratypes, are given in parentheses. Dorsal-fin rays VIII, 13; anal-fin rays III, 8; pectoral-fin rays (both sides) 15; pelvic-fin rays I, 5; principal caudal-fin rays 9+8=17; procurrent caudal-fin rays 9+9=18; pored lateral-line scales 48 (47), two additional pored scales present on base of caudal fin not included in total count; scales from lateral line to dorsal-fin origin 3 or 4 (3); gillrakers on first arch, including rudiments, 6+14-15 (6+14); upper limb with 3 rudiments + 3 rakers, lower limb with 11-13 rakers + 2-3 rudiments, total 20–21 (20); vertebrae 10 + 14.

Body proportions expressed as percentage of SL. Body depth at origin of dorsal fin 23–26 (26); body width just behind gill opening 11–14 (14); head length 37–39 (37); snout length 7.4–9.1 (9.1), relative length increasing with increasing SL; orbit diameter 9.4–12 (9.4) relative diameter decreasing with increasing SL; bony interorbital width 4.5–5.5 (5.5); upper-jaw length 16–18 (18); greatest depth of maxilla 5.0–6.1 (6.1); least caudal-peduncle depth 11–13 (13); caudal-peduncle length 22–24 (23); lengths of dorsal-fin spines: (I) 2.9–4.2 (4.2); (II) 11–12 (12); (III) 13–15 (14); (IV) 11–12 (11); (V) 6.9–10 (10); (VI) 6.9–8.2 (8.2); (VII) 5.0–7.5 (7.5); (VIII) 4.8–6.9 (6.9); longest dorsal soft ray the 11th, length 15–20 (20); length of 3rd anal-fin spine 6.9–9.3 (9.3); longest anal soft ray the 5th, length 15–17 (16); caudal-fin length 23–28 (23), relative length decreasing with increasing SL; pectoral-fin length 27–30 (27), fin reaching vertical between anus and origin of anal fin, falling short of anal fin in all specimens; pelvic-fin length 18–20 (19), fin reaching vertical through base of 6th dorsal-fin spine, well short of anus.

Interorbital region flat to slightly convex; mouth oblique, maxilla reaching vertical beyond posterior border of pupil; prominent bony projection on posteroventral corner of maxilla; lower jaw slightly projecting. Anterior nostril in thin, membranous tube, nostril situated just posterior to groove between tip of snout and premaxilla; posterior nostril a simple opening, nostril situated close to orbit (the distance approximately 1.5 nostril diameters). Lateral line strongly arched above pectoral fin, highest point below fourth and fifth dorsal-fin spines.

Trunk covered with ctenoid scales, scales becoming weakly ctenoid anteriorly and cycloid on head. Head fully scaled except over branchiostegal area. Holotype with



Figure 2. *Liopropoma santi* sp. n., type series: **A** USNM 426811, holotype, 116 mm SL, DNA #CUR 13253 **B** USNM 426813, paratype, 76.2 mm SL, DNA #CUR 13280 **C** USNM 414824, paratype, 42.0 mm SL, DNA #CUR 12314.

short column of scales on dorsal-fin spines III and IV, scales on basal portion of membranes between spines VI and VIII, three rows of scales covering basal portion of soft dorsal fin, and some scales extending distally onto soft dorsal-fin membranes; paratypes with same squamation except no scales present on spinous dorsal fin, and 42.0mm SL paratype having only basal scale rows on soft dorsal fin. In holotype and larger paratype, anal fin with two or three rows of scales basally and additional scales that extend distally onto fin membranes and cover most of fin. In smaller paratype, scales confined to basal portion of fin. Caudal fin completely scaled in holotype except for distal tips of rays; larger paratype with scales covering only proximal half of fin; smaller paratype with scales confined to basal portion of fin. Scales present on pectoral-fin base, and elongate scales present on proximal portion of fin. Scales present on pelvicfin base and on proximal portion of fin; pelvic axillary scales present.

Jaw teeth small and depressible; upper and lower jaws with bands of villiform teeth, bands widest anteriorly, largest teeth in innermost row. Vomer with a chevronshaped patch of small teeth. Palatines with several rows of small teeth in a long, narrow band. Opercle with three flattened spines, only the middle one conspicuous. Margin of upper limb of preopercle and angle with small serrations, lower limb smooth.

Prior to preservation (Figs 2, 3), background color of upper portions of trunk and caudal peduncle yellow, grading to pale pink around midbody, then to white ventrally; no abrupt transitions between those colors; many individual scales on upper half of body marked with orange spots in adults, densely so in holotype; a series of about 13 narrow, bright-white, chevron-shaped bars that point posteriorly present on lower half of trunk, series extending from just behind pectoral-fin base to vertical through center or posterior portion of anal fin; upper arms of white bars more strongly defined; nape yellow from dorsal midline ventrally to about mid-eye level (with some orange spots on scales in adults), grading anteriorly into an irregularly shaped area of purplish-pink over and behind eye, on upper portion of iris, and on snout; a yellow blotch present behind center of eye (in adults) and a smaller one present on dorsal midline of snout just anterior to orbit; iris mostly orange-yellow, grading to fine inner yellow ring; prominent, mostly deep-yellow (adults) or mostly orange (juvenile) stripe along outside of entire upper lip, this pigment spreading slightly above lip along anterior half of jaw in adults and merging with the pink/orange pigment on snout of juvenile; inside of lower lip with small blotch of yellow pigment in adults, inside of upper lip with stripe of yellow (adults) or orange (juvenile); photographic angle did not permit characterization of pigment on inside of lower lip of juvenile; lower jaw and lower two thirds of head white, with pinkish cast in holotype; in adults, dorsal fin with yellow spines and mostly white inter-spinous membranes; soft dorsal-fin rays yellow, membrane between anterior rays yellow, and membrane between rays of remainder of fin with small to large pale area centrally, size of pale area increasing posteriorly such that membrane between posteriormost rays completely pale; some rays and membranes in posterior portion of soft dorsal fin with pale rose pigment in smaller adult; a thin white margin extending along outer edge of entire dorsal fin, this margin appearing blue-white when fish photographed against black background (Fig. 3); in juvenile, inter-spinous membranes of dorsal fin mostly pale and soft dorsal mostly pale except for yellow stripe at the base and yellow stripe near outer margin of fin; caudal fin mostly yellow in holotype, central portion of fin with pale outer margin and with pale to pinkish-orange membranes between rays; thin pinkish-orange stripe present along dorsal and ventral margins of fin; distal tip of lower lobe with reddish-black blotch, a few thin streaks of black extending proximally from this blotch; pigment on caudal fin of smaller adult similar but with less pinkish-orange pigment, and caudal fin of juvenile mostly clear with a large, oval-shaped, oblique yellow blotch on outer half of both upper and lower



Figure 3. *Liopropoma santi* sp. n., USNM 426811, holotype, 116 mm SL (photographed against a black background).



Figure 4. In-situ photograph of *Liopropoma santi* sp. n., taken from the *Curasub* submersible at 204 m on a reef slope off Jan Theil Bay, Curaçao, 5 Nov 2013. Photo courtesy of Substation Curaçao.

lobes; dark spot on distal portion of ventral caudal lobe relatively larger in juvenile; anal fin white, with faint pinkish-yellow streak on first through fifth rays in holotype, little or no color in smaller adult and juvenile; pelvic fin white; pectoral fin translucent with pale pinkish-orange cast; general coloration most intense in the holotype and least intense in the juvenile.

In alcohol (see Fig. 6A), body pale, the only pigment a dark blotch on distal tip of ventral caudal-fin lobe.

Distribution. Known only from Curaçao, southern Caribbean.

Habitat. Off Curaçao, *L. santi* is found from 182–241 m inhabiting rocky slopes and ledges. It retreats into small caves and crevices when approached and illuminated by the submersible. Figure 4 shows an in-situ photograph taken from the *Curasub* submersible at 204 m on a reef slope off Jan Theil Bay, Curaçao.

Etymology. The specific name honors Roger Sant, who participated in the *Cu-rasub* submersible dive at Playa Forti during which the USNM 426813 paratype was collected. Roger and Victoria Sant have provided generous funding to the Smithsonian Institution's National Museum of Natural History for ocean-related activities.

Common name. "Spot-tail golden bass" is in reference to the dark spot on the lower lobe of the caudal fin, which, along with other characters, distinguishes *L. santi* from the two other species of western Atlantic *Liopropoma* that have predominantly golden coloration, *L. aberrans* and *L. olneyi*.

Comparisons. Counts and measurements of the three western Atlantic "golden basses" collected off Curaçao, *L. santi, L. aberrans*, and *L. olneyi*, are given in Table 2, representative images of the three are provided in Figure 5, and a summary of major differences among them appears in Table 3. An image of a freshly collected specimen of a species of the related genus *Bathyanthias* is also included in Figure 5 for comparative purposes. *Liopropoma santi* is easily distinguished from the others by color in life, especially by the presence of a yellow or orange stripe externally on the upper lip, a series of white chevron-shaped markings on the ventral portion of the trunk, and the reddish-black blotch on the distal portion of the lower caudal-fin lobe. The last also visually distinguishes *L. santi* from *L. aberrans* and *L. olneyi* in preservative. *Liopropoma santi* is further distinguished from both of those species by having more dorsal-fin rays, more gill rakers on the first arch, and usually a larger eye (Table 2). From *L. aberrans, L. santi* is further distinguished by having more pectoral-fin rays, a narrower body at the dorsal-fin origin, a narrower caudal peduncle, longer fourth-sixth dorsal-fin spines, and a more shallow indentation in the spinous dorsal fin (Tables 2, 3).

Baldwin and Johnson (2014) discussed the status of *L. aberrans*, which was described from a single specimen collected off Cuba in the 19th century (Poey 1860) and redescribed from a single specimen collected off the Bahamas in the 20th century (Robins 1967). They noted differences in the descriptions of color patterns of the two specimens and numbers of dorsal-fin rays (IX, 12 in Poey's *L. aberrans*, VIII, 12 in Robins' *L. aberrans*), and they questioned whether or not the two specimens represent the same species. Specimens of *L. aberrans* collected off Curaçao ("Curaçao *L. aberrans*") share with the Bahamas *L. aberrans* the same dorsal-fin count, general body shape, and color pattern, although Baldwin and Johnson (2014) noted some differences in the color pattern. Curaçao *L. aberrans* have 17–18 gill rakers on the first arch (Table 2), whereas Robins (1967) reported 14 for the Bahamas specimen; however, as noted by Baldwin and Johnson (2014), Robins' count only included the rudimentary pads on the upper limb. Examination of the Robins' Bahamas specimen (UMML 22324) indicates that there are four rudimentary pads on the lower limb, and thus the total number of gill rakers on the first arch is 18.

	L. santi	L. santi	L. santi	L. olneyi	L. aberrans
Museum Catalog Numbers	USNM 426811 Holotype	USNM 426813 Paratype	USNM 414824 Paratype	See Appendix	See Appendix
SL (mm)	116	76.2	42.0	53.2-84.3	64.8-116
Dorsal Fin	VIII, 13	VIII, 13	VIII, 13	IX, 11	VIII, 12
Pectoral Fin	15	15	15	14-15	14
Gill Rakers on First Arch	6+14=20	6+14=20	6+15=21	5-6+12-13=17-19	5-6+11-13=17-18
Orbit diameter	9.4	10	12	7.8–9.4	7.4–8.7
Body depth at dorsal- fin origin	26	25	23	20–24	27–29
Least depth of caudal peduncle	13	13	11	13–15	16–17
Length of dorsal-fin spine IV	11	11	12	9.7–12	8.1–9.7
Length of dorsal-fin spine V	9.5	10	6.9	8.3–9.3	3.7–5.6
Length of dorsal-fin spine VI	8.2	7.9	6.9	7.3–8.9	3.6–5.6

Table 2. Selected counts and measurements for the type series of *Liopropoma santi* sp. n., *L. aberrans* from Curaçao, and *L. olneyi*. Measurements are in percentages of SL. Data for *L. aberrans* are from Curaçao specimens examined in this study, those for *L. olneyi* are from Baldwin and Johnson (2014).

Table 3. Summary of differences in morphology and depth ranges among the three golden-colored *Lio-propoma* species off Curaçao.

Character	<i>L. santi</i> sp. n.	L. olneyi	L. aberrans
Relative body depth	Shallow (23-26% SL)	Shallow (20-24% SL)	Deeper (27–29% SL)
Dorsal fin indentation	Moderate (6 th spine 7–8% SL)	Weak (6 th spine 7–9% SL)	Strong (6 th spine 4–6% SL)
Dorsal-fin rays	VIII, 13	IX, 11	VIII, 12
Gill rakers on first arch	20-21	17–19	17–18
Orbit diameter (% SL)	9.4–12	7.8–9.4	7.4–8.7
White flank chevrons	yes	no	no
Body ground colors	yellow over white	yellow over white	yellow over orange
Yellow stripe through eye	no	yes	yes
Yellow-orange upper lip	yes	no	no
Yellow spots on body	no	adult & juvenile	juvenile only
Dark spot on lower caudal-fin lobe	yes	no	no
Depth range (m)	181–241	133–193	98–149

Curaçao and Bahamas *L. aberrans*, however, appear to have different depth preferences, with Robins' *L. aberrans* occurring deeper—229 m. At Curaçao, *L. aberrans* was collected between 98 and149 m and observed by us only within that depth range during nearly 100 submersible dives over a three-year period. This is unlikely to be due to effects of differences in habitat availability at the two locations, as *L. santi* and *L. olneyi* occur at deeper depths than *L. aberrans* at Curaçao.



Figure 5. Comparison of the three species of "golden basses" off Curaçao and *Bathyanthias* sp. from Panama: **A** *Liopropoma santi* sp. n., USNM 426811, holotype, 116 mm SL, DNA #CUR 13280 **B** *L. aberrans*, USNM 426807, 102 mm SL, DNA #CUR 12226 **C** *L. olneyi*, USNM 426805, holotype, 84.3 mm SL, DNA #CUR 13200 **D** *Bathyanthias* sp., USNM 407791, 110 mm SL, DNA #MOC 11791.



Figure 6. Comparison of *Liopropoma* and *Bathyanthias:* **A** *L. santi* sp. n., USNM 426811, holotype, 116 mm SL (photographed after preservation) **B** *B. cubensis* (Schultz 1958), USNM 158138, holotype, 80.3 mm SL. Photos by Sandra Raredon.

Poey (1860) did not provide depth data or a gill-raker count for his 115-mm SL specimen from Cuba. Curaçao *L. aberrans* differs from the Cuban *L. aberrans* in dorsal-fin count and certain aspects of color pattern, but fish from those two sites share the presence of yellow spots on the cheek (sometimes lacking in juvenile Curaçao *L. aberrans*), spots that were not mentioned by Robins (1967) for the 112-mm SL Bahamas *L. aberrans*. The whereabouts of the holotype of *L. aberrans* are unknown (Eschmeyer 2013), and, in the absence of additional material from the type locality for comparative purposes, we follow Baldwin and Johnson (2014) in tentatively recognizing the specimens from Cuba, Bahamas, and Curaçao as *L. aberrans*. As noted by Baldwin and Johnson (2014), a digitized copy of a color photograph of a specimen of *L. aberrans* from Jamaica taken and provided by Patrick Colin shows a color pattern nearly identical to that of Curaçao *L. aberrans*. Should Poey's *L. aberrans* prove to be distinct from specimens from the Bahamas, Curaçao, and Jamaica, one or more new species will need to be recognized.

Liopropoma santi differs from Poey's and Robins' *L. aberrans* in number of dorsal-fin rays (VIII, 13 vs. IX, 12 and VIII, 12, respectively) and shape of dorsal fin (with only a moderate indentation in spinous dorsal fin in *L. santi*, deep indentation in the others). It further differs from Robins' *L. aberrans* in numbers of pectoral-fin

Table 4. Dorsal-fin counts of western Atlantic Liopropomini fishes. Data for *Bathyanthias atlanticus*, *B. cubensis*, and *B. mexicanus* are from Schultz (1958); for *Liopropoma aberrans* (Cuba) Poey (1860); for *L. aberrans* (Bahamas) Robins (1967); for *L. carmabi*, *L. eukrines*, *L. mowbrayi*, *L. rubre* Randall (1963); and for *L. olneyi* Baldwin and Johnson (2014).

	SPINES			SOFT RAYS			
	VIII	IX	11	12	13	14	15
Bathyanthias atlanticus	+					+	
Bathyanthias cubensis	+				+		
Bathyanthias mexicanus	+					+	+
Bathyanthias roseus ¹	+					+	
Liopropoma aberrans (Curaçao)	+			+			
Liopropoma aberrans (Cuba)		+		+			
Liopropoma aberrans (Bahamas)	+			+			
Liopropoma carmabi	+			+	+		
Liopropoma eukrines	+			+			
Liopropoma mowbrayi	+			+			
Liopropoma olneyi		+	+				
Liopropoma rubre	+			+			
<i>Liopropoma santi</i> sp. n.	+				+		

¹As noted by Baldwin and Johnson (1993), Günther (1880) gave IX, 14 as the dorsal-fin count for *B. roseus*, but their examination of a radiograph of the type specimen indicates that it has VIII dorsal spines.

rays (15 vs. 14) and gill rakers on the first arch (20–21 vs. 17–18), and color pattern (presence of diagnostic color features of *L. santi*-see Diagnosis-vs. absence). From other western Atlantic *Liopropoma* (*L. carmabi* [Randall 1963], *L. eukrines* [Starck and Courtenay 1962], *L. mowbrayi* [Woods and Kanazawa 1951], *L. rubre* Poey 1861), *L. santi* differs most notably in color pattern (Fig. 1) and in having VIII, 13 dorsal-fin rays (vs. VIII, 12 in all except one specimen of *L. carmabi* with VIII, 13–Table 4).

Counts of *L. santi* closely match those of *Bathyanthias cubensis* (Schultz, 1958) in having VIII, 13 dorsal-fin rays; III, 8 anal-fin rays; 15 pectoral-fin rays; and 20–21 gill rakers on the first arch. *Liopropoma santi* has 47–49 lateral-line scales, whereas *B. cubensis* has 46–47. The two species are otherwise very different. *Liopropoma santi* has a shallower trunk (body depth 23–26% SL and caudal-peduncle depth 11–13% SL in *L. santi* vs. 28–32% SL and 14–15% SL, respectively, in *B. cubensis* – Schultz, 1958), and *L. santi* has a single blotch of dark pigment on the distal portion of the lower caudal-fin lobe vs. dark pigment on the distal ends of all caudal-fin rays. Like other species of *Bathyanthias*, the dorsal profile of the head in *B. cubensis* is convex (vs. usually straight in *Liopropoma*—although there may be a bump on the snout and the profile may be slightly convex in large specimens of *Liopropoma*); there is little indentation in the margin of the spinous dorsal fin (vs. larger indentation); the posteroventral corner of the maxilla has a weakly developed hook-like process (vs. well developed in *Liopropoma* – see Randall and Taylor [1988] and Baldwin and Johnson [1993]); and in *Bathyanthias*, the anterior portion of the lateral line is broadly curved over the pectoral fin (vs.

sharply curved in *Liopropoma*). Differences between *L. santi* and *L. cubensis* can be seen in Figure 6, and the generic characters listed above can be seen in Figures 5 and 6. The depth range of *B. cubensis* is greater than that of *L. santi*, 183–411 m vs. 182–241 m.

Discussion and conclusions

A combination of morphological and genetic differences supports the recognition of L. santi as a valid new species of Liopropoma. Liopropoma santi inhabits depths of 182-241 m off Curaçao, making it the deepest known Liopropoma species in the western Atlantic (Fig. 7). The shallower portion of its depth range overlaps the deeper portion of the depth range of *L. olneyi* (133–193 m), but with the exception of Robins' (1967) specimen of L. aberrans from the Bahamas (229 m), no other western Atlantic Liopropoma species occur within the depth range of L. santi. A preliminary phylogeny of western Atlantic Liopropoma based on parsimony analysis of the COI data is shown in Figure 8. In that phylogeny, the three species that inhabit depths of 3–135 m (*L. rubre*, L. carmabi, and L. mowbrayi) form a monophyletic group that is sister to a clade comprising two species that inhabit depths of 30-150 m (L. eukrines and L. aberrans from Curaçao). Those clades combined are sister to a clade comprising the deepest western Atlantic Liopropoma (L. olneyi and L. santi, 133-241 m) plus two species of the genus Bathyanthias (B. mexicanus [Schultz 1958] and a putative new species from Panama) that were collected at 143–259 m. Two additional species of Bathyanthias, B. atlanticus [Schultz, 1958] and B. cubensis (not available for inclusion in the molecular phylogenetic analysis), are known from 82–411 m, and the depth range of non-Curacao L. aberrans (also not available for inclusion in the phylogenetic analysis) is 89-230 m (Robins 1967, Ocean Biogeographic Information System [OBIS] - http://www.iobis. org/, Fishnet 2 - http://www.fishnet2.net/).

The COI data provide excellent support for the monophyly of species of western Atlantic Liopropoma but poor support for clades within the genus (see bootstrap values in Fig. 8). Nevertheless, the strict consensus (Fig. 8) suggests that western Atlantic liopropomins are monophyletic with respect to Indo-Pacific Liopropoma (L. lunulatum, L. tonstrinum, and L. pallidum in Fig. 8). A more robust phylogenetic hypothesis is needed that is derived from additional genes and more Indo-Pacific species of Liopropoma, but the COI data suggest a relationship between depth and monophyletic clades in western Atlantic Liopropomini that warrants further investigation. Members of the three clades of western Atlantic liopropomins identified in the phylogeny show a tendency to occupy different depth strata (3-135 m, 30-150 m, and 82-411 m). Based on our few specimens, it appears that L. santi has larger eyes than its sister species, L. olneyi (Table 3), which may represent an adaptation allowing L. santi to extend its range to greater depths. Among the three golden basses at Curaçao (L. aberrans, L. olneyi, L. santi), L. aberrans has the shallowest range and shows a tendency to have the smallest eyes (Table 3). Adaptation to life at different depths may have been involved in the speciation of this co-occuring species group. It may also be involved in the di-



Figure 7. Depth distributions of western Atlantic *Liopropoma* and *Bathyanthias* species that were included in the phylogenetic analysis (see Fig. 8). Photographs of *L. rubre* and *L. mowbrayi* by James Van Tassell and Ross Robertson.

vergence between *L. mowbrayi* and *L. rubre*, which represent sister species that show only partial overlap in their depth ranges (Fig. 7) but broadly overlapping geographic ranges that incorporate most of the Caribbean and adjacent areas. Adaptation to use of different depth strata may also have been involved in the initial diversification of western Atlantic liopropomins into three clades that now occupy the same geographic area. Such parapatric ecological speciation, in which species diverge along environmental gradients, has been proposed for other marine fishes including *Halichoeres* (Rocha et al. 2005) and *Sebastes* (Ingram 2011). In *Sebastes*, Ingram (2011) found a strong signal of speciational evolution in depth habitats and in traits apparently related to life at different depths, such as eye size.

Conversely, the sister species *L. eukrines* and *L. aberrans* overlap substantially in depth range but show a significant amount of geographic separation: *L. eukrines* is largely restricted to the Gulf of Mexico and southeastern USA, whereas *L. aberrans* is primarily Caribbean. However, there is one inconsistency in this pattern of either geographic or depth segregation among members of the same clade: *L. carmabi* and both species in its sister group, *L. rubre* and *L. mowbrayi*, have both geographic- and depth ranges that broadly overlap. Liopropomins have pelagic larvae, and allopatric speciation might be facilitated by larval dispersal to new areas. Possibly both ecological and allopatric speciation have occurred in the group, but, if so, more information on depth and geographic distributions, morphological traits associated with life at different depths, and evolutionary relationships is needed to estimate their relative roles. Depth and morphological information for the three members of the *L. rubre* clade collected at the same geographic location would be highly relevant in this regard. At



Figure 8. The strict consensus of a maximum parsimony analysis of the COI region among western Atlantic *Liopropoma* and related taxa. The tree was rooted on *Scorpaena plumieri*, (CUR11401), and the non-liopropomin serranids *Rypticus carpenteri* (TOB9102) and *Grammistes sexlineatus* (MBIO1671) were included as additional outgroups. Photographs of *L. rubre* and *L. mowbrayi* by James Van Tassell and Ross Robertson; photos of *L. pallidum* and *L. lunulatum* by Jeffrey Williams (from Encyclopedia of Life); photo of *L. tonstrinum* by Richard Winterbottom (from Encyclopedia of Life).

Puerto Rico all three species in that clade occur on the same mesophotic reefs, where they reach the same maximum depth (Bejarano et al 2014). At Curaçao Adriaan Schrier, who operates Substation Curaçao, has been actively collecting all three species for many years using a combination of traditional SCUBA, mixed gas SCUBA, and the *Curasub*. He provided (personal communication March 2014) the following information for that location: *L. rubre* occurs at 12–55 m, *L. mowbrayi* at 12–135m, and *L. carmabi* at 25–100m. He also noted that while *L. mowbrayi* and *L. carmabi* are found in areas with small-scale coral and rock shelter and rubble, *L. rubre* is restricted to caves in large scale coral structures and is much more secretive than the other two species. These observations indicate that members of the *L. rubre* clade show some degree of depth segregation within a site, as well as microhabitat segregation.

The phylogeny (Fig. 8) further suggests the need to reanalyze generic relationships within the Liopropomini, as *Bathyanthias* is embedded within western Atlantic *Liopropoma*. Morphologically, *L. santi, L. olneyi*, and *Bathyanthias* differ from other western

Atlantic *Liopropoma* in having a smaller indentation in the margin of the dorsal fin, and those liopropomins lack body stripes and have similar pale orange/yellow/rose coloration. Four species of *Bathyanthias* have been described – *B. atlanticus* (Schultz, 1860), *B. cubensis* (Schultz, 1860), *B. mexicanus* (Schultz, 1860), and *B. roseus* Günther 1880. Of those, only *B. mexicanus* from the Gulf of Mexico (FWRI 20709) was available for inclusion in our phylogenetic analysis. The other *Bathyanthias* species included, which may represent an undescribed species, is from Central America - Panama (USNM 407791, MOC 11791). Its combination of dorsal-, pectoral, lateral-line, and gill-raker counts do not match any other known species of *Bathyanthias*.

Of the three western Atlantic species of *Liopropoma* with depth distributions entirely below depths accessible using conventional scuba gear – *L. aberrans, L. olneyi*, and *L. santi*—two have been discovered only recently through submersible diving to 300 m off Curaçao in the southern Caribbean (*L. olneyi* and *L. santi*). More exploration of western Atlantic tropical mesophotic and other deep-reef depths is needed to fully document fish diversity even in well-studied taxonomic groups such as the Serranidae.

Comparative material

Specimens, color images, or both, were examined of all western Atlantic liopropomin material listed in the Appendix. The following non-Curaçao *L. aberrans* material was examined: UF 222324, 1 specimen, Bahamas; UF 230721, 1, Jamaica; UF 230254, 1, French Guiana.

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Appendix

Links between DNA voucher specimens, GenBank accession numbers, and cytochrome c oxidase subunit I (COI) sequences of *Liopropoma santi* sp. nov., related Liopropomini, and outgroup taxa.

Catalog Number/DNA Number	GenBank No.	GenSeq Designation
Liopropoma santi sp. n.		·
USNM 426811, CUR 13253, Holotype	KJ526147	Geneseq-1 COI
USNM 426813, CUR 13280, Paratype	KJ526148	genseq-2 COI
USNM 414824, CUR 12314, Paratype	KJ526146	genseq-2 COI
Liopropoma olneyi		· · ·
USNM 426805, CUR 13200, Holotype	KF770874	genseq-1 COI
USNM 406130, CUR 11130, Paratype	KF770856	genseq-2 COI
USNM 414828, CUR 12060, Paratype	KF770862	genseq-2 COI
USNM 426808, CUR 13225, Paratype	KF770876	genseq-2 COI
USNM 426809, CUR 13227, Paratype	KF770878	genseq-2 COI
USNM 426810, CUR 13244, Paratype	KF770879	genseq-2 COI
USNM 426815, CUR 13290, Paratype	KF770882	genseq-2 COI
USNM 422698, CUR13106, Paratype	KF770872	genseq-2 COI
USNM 426868, FLST 5001, Paratype (larva)	KF770883	
Liopropoma aberrans		
USNM 406001, CUR 11001	KF770853	genseq-4 COI
USNM 406025, CUR 11025	KF770855	genseq-4 COI
USNM 426806, CUR 13218	KF770875	genseq-4 COI
USNM 426807, CUR 13226	KF770877	genseq-4 COI
USNM 426814, CUR 13259	KF770880	genseq-4 COI
USNM 426812, CUR 13260	KF770881	genseq-4 COI
Liopropoma carmabi		
USNM 406374, CUR 11374	KF770858	genseq-4 COI
USNM 414825, CUR 12032	KF770861	genseq-4 COI
USNM 414826, CUR 12070	KF770863	genseq-4 COI
USNM 414827, CUR 12071	KF770864	genseq-4 COI
USNM 413959, CUR 13084	KF770866	genseq-4 COI
USNM 413960, CUR 13085	KF770867	genseq-4 COI
USNM 413961, CUR 13086	KF770868	genseq-4 COI
USNM 422694, CUR 13099	KF770869	genseq-4 COI
USNM 422687, CUR 13108	KF770873	genseq-4 COI
Liopropoma eukrines		
SIO 01-11, MCgroup 3333	KF770885	genseq-4 COI
Liopropoma mowbrayi		
USNM 420350, BLZ 5325	JQ840569	genseq-4 COI
USNM 420349, BLZ 5326	JQ840570	genseq-4 COI
BLZ 7720 (photo voucher only)	JQ841243	genseq-5 COI
USNM 406015, CUR 11015	KF770854	genseq-4 COI
USNM 406131, CUR 11131	KF770857	genseq-4 COI
USNM 406386, CUR 11386	KF770859	genseq-4 COI
USNM 414815, CUR 12315	KF770865	genseq-4 COI

Catalog Number/DNA Number	GenBank No.	GenSeq Designation
USNM 422684, CUR 13101	KF770870	genseq-4 COI
USNM 422675, CUR 13103	KF770871	genseq-4 COI
Liopropoma rubre		
USNM 414697, BAH 9032	KF770852	genseq-4 COI
USNM 419340, BLZ 5117	JQ840571	genseq-4 COI
USNM 416331, BLZ 6236	JQ840899	genseq-4 COI
USNM 416379, BLZ 6377	JQ840900	genseq-4 COI
USNM 416009, BLZ 7806	JQ841244	genseq-4 COI
USNM 415207, BLZ 8050	JQ841640	genseq-4 COI
USNM 415226, BLZ 8095	JQ841637	genseq-4 COI
USNM 415180, BLZ 8153	JQ841638	genseq-4 COI
USNM 415181, BLZ 8154	JQ841641	genseq-4 COI
USNM 415244, BLZ 8167	JQ841639	genseq-4 COI
USNM 414498, CUR 8332	JQ842192	genseq-4 COI
USNM 414499, CUR 8333	JQ842193	genseq-4 COI
Liopropoma lunulatum (Pacific)		
MBIO 1710 (no photo or specimen voucher)	JQ431889	no classification
MNHN 2008-1023, MBIO 1472	JQ431888	genseq-4 COI
Liopropoma tonstrinum (Pacific)		
USNM 425632, MOOP37	KJ526149	genseq-4 COI
USNM 425630, MOOP38	KJ526150	genseq-4 COI
Liopropoma pallidum (Pacific)		
MNHN 2009-0793, MBIO 961	JQ431890	genseq-4 COI
MNHN 2009-0794, MBIO 962	JQ431891	genseq-4 COI
Bathyanthias mexicanus		
FWRI 20709 (DNA number same)	KF770884	genseq-4 COI
Bathyanthias sp.		
USNM 407791, MOC 11791	KF770886	genseq-4 COI
Outgroup Taxa		
Grammistes sexlineatus		
MNHN 2008-1105, MBIO 1671	JQ431776	genseq-4 COI
Rypticus carpenteri		
USNM 401296, TOB 9102	JN828097	genseq-4 COI
Scorpaena plumieri		
USNM 406401, CUR 11401	KF770860	genseq-4 COI

RESEARCH ARTICLE



A new species of Dysanabatium Bernhauer and additional records of D. jacobsoni Bernhauer (Coleoptera, Staphylinidae, Paederinae)

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thttp://zoobank.org/6CDD4A22-46AC-4DAF-8409-6D1922AE5D81
http://zoobank.org/21DBB891-9080-4061-A62D-6FCD51BCE48A
http://zoobank.org/BBACC7AE-9B70-4536-ABBE-54183D2ABD45
http://zoobank.org/FBE4FA1F-5BCF-405E-98C1-4F86894643EA

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Abstract

Dysanabatium hainanense Peng & Li, **sp. n.** (Hainan: Wuzhi Shan, Diaoluo Shan) is described and illustrated. Additional records of *D. jacobsoni* Bernhauer, 1915 are reported. The habitus, the sexual characters, and the distribution of this enormously variable species are illustrated.

Keywords

Coleoptera, Staphylinidae, Dysanabatium, new species, new records, China

Introduction

The paederine genus *Dysanabatium* Bernhauer, 1915 is distributed in the Oriental and southeastern Palaearctic region and was previously represented by seven species. Only one species, *D. jacobsoni* Bernhauer, 1915, had been reported from China (Yunnan) (Rougemont 1997). According to Rougemont (1997), *Dysanabatium* species inhabit river banks in woodland habitats.

A study of *Dysanabatium* material from southwestern China, Laos, and Vietnam yielded one species new to science and numerous records of *D. jacobsoni*.

Material and methods

The examined material is deposited in the following public and private collections:

NHMB	Naturhistorisches Museum Basel, Switzerland (M. Geiser, I. Zürcher)
NMP	National Museum of Natural History, Praha, Czech Republic (J. Hájek)
SNUC	Insect Collection of Shanghai Normal University, Shanghai, China
cAss	Private collection Volker Assing, Hannover, Germany

The morphological studies were conducted using Stemi SV 11 (Zeiss Germany) and Olympus CX31 microscopes, and a Jenalab compound microscope (Carl Zeiss Jena). The images were prepared using Nikon Coolpix 995, Canon EOS 70D (with an MP-E 65 macrolens), and Canon G12 cameras. The map was created using MapCreator 2.0 (primap) software.

The following abbreviations are used in the text, with all measurements in millimeters:

Body length (BL)	length of body from the anterior margin of the mandibles
	(in resting position) to the abdominal apex.
Forebody length (FL)	length of forebody from the anterior margin of the mandi-
	bles to the posterior margin of elytra at suture.
Head length (HL)	length of head from the anterior margin of the frons to the
	posterior margin of the head.
Head width (HW)	maximum width of head (including eyes).
Antenna length (AnL)	length of antenna from the basis of the antenna to the apex.
Pronotum length (PL)	length of pronotum along midline.
Pronotum width (PW)	maximum width of pronotum.
Elytral length (EL)	at the suture from the apex of the scutellum to the posterior
· -	margin of the elytra (at the sutural angles).
Aedeagus length (AL)	length of the aedeagus from the apex of the ventral process
- •	to the base of the aedeagal capsule.

Species description and additional records

Dysanabatium hainanense Peng & Li, sp. n.

http://zoobank.org/951C1265-22A1-4186-8D42-FF274643C0AF http://species-id.net/wiki/Dysanabatium_hainanense Figs 1A, 2, 5

Description. Measurements (in mm) and ratios: BL 5.89–6.43, FL 3.34–3.45, HL 0.80–0.84, HW 1.05–1.15, AnL 1.94–2.08, PL 0.93–0.98, PW 0.78–0.83, EL 1.11–1.19, AL 0.89–0.93, HL/HW 0.73–0.76, HW/PW 1.35–1.39, HL/PL 0.85–0.86, PL/PW 1.16–1.19, EL/PL 1.19–1.23, diameter of eye: 0.50–0.54.

Habitus as in Fig. 1A. Body entirely black, glossy, devoid of microsculpture; labial palpi and segments I, II, IV of maxillary palpi brownish yellow, segment III of maxillary palpi infuscate; antennae blackish brown at base, gradually becoming paler towards the reddish brown apices; basal halves of femora brownish yellow, distal halves gradually infuscate; tibia and tarsi infuscate.

Head transverse, eyes very large and prominent, temples convergent posteriorly in almost straight line, posterior angles inconspicuous; punctation moderately coarse and dense, sparser in median dorsal portion. All antennomeres oblong.

Pronotum with strongly convex lateral margins in dorsal view; punctation shallow, sparser than that of head; impunctate midline broad.

Elytra with coarse simple punctation arranged in longitudinal series in anterior seven tenths, becoming finer and shallower posteriorly; pubescence golden, erect, conspicuous. Hind wings fully developed.

Abdomen strongly dilated from segments III to apex of segment VI, segment VII convexly tapering posteriorly; segments III–VII with strongly reflexed paratergites; punctation sparse and fine; pubescence fine and pale, with interspersed longer, darker pubescence, especially posteriorly.

Protarsi very strongly, slightly asymmetrically dilated in both sexes; profemora with bases slender, very strongly, symmetrically incrassate to apical third; outer surfaces of tibiae with pale pubescence. First metatarsomere longer than second, subequal to or slightly shorter than fifth; fourth tarsomere simple.

Male. Posterior margin of tergite VIII (Fig. 2D) broadly convex; sternites III– VI unmodified; posterior margin of sternite VII broadly concave; sternite VIII (Fig. 2E) symmetric and strongly tapering posteriorly, with moderately deep, subtriangular posterior emargination; aedeagus as in Figs 2F, G, ventral process moderately stout



Figure I. Habitus of *Dysanabatium* spp., **A** *D. hainanense* **B–H** *D. jacobsoni* (**B–D** Yunnan; **E** Guangxi; **F–H** Hainan). Scales: 1.0 mm.

and apically acute; internal sac with simple membranous structures and an apically rounded, weakly sclerotized structure.

Female. Posterior margin of tergite VIII (Fig. 2A) asymmetrically and broadly convex; sternite VIII (Fig. 2B) longer than that of male, posterior margin broadly convex; tergite IX (Fig. 2C) with short antero-median portion and moderately long postero-lateral processes; tergite × 5.0 times as long as antero-median portion of tergite IX (Fig. 2C).

Distribution and natural history. The type locality is situated in the Wuzhi Shan and Diaoluo Shan, central Hainan. The specimens from Wuzhi Shan were sifted from flood debris, moss, leaf litter and soil near streams in evergreen broad leaved forest, partly together with *Dysanabatium jacobsoni* Bernhauer, 1915 (Fig. 5).

Etymology. The specific epithet is derived from Hainan, the province where the type locality is situated.

Comparative notes. In external (transverse head; elongate elytra; bicolorous femora) and the male sexual characters (shapes and chaetotaxy of the male sternites VIII),



Figure 2. *Dysanabatium hainanense*. **A** female tergite VIII **B** female sternite VIII **C** female tergites IX–X. **D** male tergite VIII **E** male sternite VIII **F** aedeagus in ventral view **G** aedeagus in lateral view. Scales: 0.5 mm.

Dysanabatium hainanense resembles *D. jacobsoni* Bernhauer, 1915 and *D. birmana* Cameron, 1931. The new species is distinguished from the former by less prominent posterior angles of the head, somewhat larger eyes, the somewhat shorter fifth meta-tarsomere, and the morphology of the aedeagus (different shape of ventral process and stouter sclerotized structure in internal sac). For illustrations of *D. jacobsoni* see Figs 1B–H, 3A–P, 4A–F and Rougemont (1997: 323, Fig. 1; 324, Figs 3a–5). It differs from *D. birmana* by greater body size, the transverse head, the larger eyes, the darker and much longer antennae, the black and glossy pronotum, the denser punctation of the elytra, the larger aedeagus, the somewhat stouter ventral process in lateral view and the weakly sclerotized internal sac of the aedeagus. For illustrations *D. birmana* see Rougemont (1997: 324, Fig. 6).

Dysanabatium jacobsoni Bernhauer, 1915

http://species-id.net/wiki/Dysanabatium_jacobsoni Figs 1B–H, 3–6

Material studied (89 33, 104 99, 358 exx.). China: Yunnan: 40 33, 78 99, Nabanhe County, Naban, 22°10'N, 100°40'E, 650 m, 7.i.2004, Li & Tang leg. (SNUC); 10 33, 8 99, Nabanhe County, Nabanhe N. R., Manfei, 22°09'N, 100°41'E, 650 m, 9.i.2004, Li & Tang leg. (SNUC); 1 Å, Nabanhe County, Nabanhe N. R., 620 m, 18.ix.2008, Hu & Tang leg. (SNUC); 4 ♂♂, 3 ♀♀, Nabanhe County, Nabanhe N. R., 22°10'N, 100°39'E, 720 m, 22.ix.2008, Hu & Tang leg. (SNUC); 25 33, 9 ♀♀, Nabanhe County, Mandian, 22°07'N, 100°41'E, 700 m, 12.i.2004, Li & Tang leg. (SNUC); 3 QQ, Xishuangbanna, Xiaonuoyouxiazhai, 22°12'N, 100°28'E, 800 m, 6.i.2004, Li & Tang leg. (SNUC). Guangxi: 1 ♂, Jinxiu County, Dayaoshan N. R., 24°08'N, 110°11'E, 850–900 m, 24.vii.2011, Peng leg. (SNUC). Jiangxi: 1 3, Jinggang Shan, Xiangzhou env., 26°36'N, 114°16'E, 370 m, forested stream valley, 26.iv.2011, Fikáček & Hájek leg. (NMP). **Hainan:** 4 ♂♂, 2 ♀♀, 24 km NE Wuzhishan, Wuzhi Shan Guanshandian, 18°53'N, 109°40'E, 650 m 19.iv.2012, Peng & Dai leg. (SNUC); 2 ♂♂, Changjiang County, Bawangling, 19°07'N, 109°07'E, 450–650 m, 13.iv.2010, Zhu leg. (SNUC); 1 3, Lingshui County, Diaoluo Shan, 18°43'N, 109°52'E, 900 m, 18.xi.2006, Li leg. (SNUC); 1 Q, Lingshui County, Diaoluo Shan, 18°43'N, 109°51'E, 1000 m, 20.iv.2010, Yuan leg. (SNUC).

Vietnam: 320 exx., Quang Binh province, Vietnam-Laos border region, 1 km N Cha Lo, 17°41'N, 105°46'E, 11.–24.iv.2010, Dembický leg. (NHMB, cAss).

Laos: 9 exx., Khammouan province, Ban Khoun Ngeun, 18°07'N, 104°29'E, 200 m, 24.–29.iv.2001, Kubáň leg. (NHMB, cAss); 4 exx., Bokeo province, 5 km W Ban Toup, Bokeo Nature Reserve, 20°27–28'N, 100°45'E, 500–700 m, 4.–18.v.2011, Brancucci et al. leg. (NHMB, cAss); 13 exx., Louangphrabang province, 5 km W Ban Song Cha, 20°33–34'N, 102°14'E, 1200 m, 1.–16.v.1999, Kubáň leg. (NHMB, cAss); 1 ex., Louangphrabang province, Thong Khan, 20°33–34'N, 102°14'E, 750 m, 11.–21.v.2002, Kubáň leg. (NHMB); 6 exx., Oudomxai province, 17 km ENE Oudom Xai, 20°45'N, 102°09'E, 1100 m, 1.–9.v.2002, Kubáň leg. (NHMB, cAss); 3 exx., Bolikhamxai province, 8 km NE Ban Nape, 18°21'N, 105°08'E, 600 m, 1.–18.v.2001, Kubáň leg. (NHMB, cAss); 1 ex., Louangnamtha province, between Namtha and Muang Sing, 21°09'N, 101°19'E, 900–1200 m, 5.–31.v.1997, Kubáň leg. (NHMB); 1 ex., Champasak province, Bolaven plateau, Muang Paxong, Ban Thongvay, 15°14'N, 106°32', 1000–1200 m, 7.–16.vi.2008, Solodovnikov & Pedersen leg. (cAss).

Comment. The original description of *D. jacobsoni* is based on an unspecified number of syntypes from Java (Bernhauer 1915). Two syntypes, a female without head and pronotum labelled as "Type" and a male labelled as "Cotype" from the Bernhauer collection were studied by Rougemont (1997). For illustrations of the habitus and the male and female sexual characters see Figs 1B–H, 3A–P, and 4.

As was already observed by Rougemont (1997), this species is subject to enormous intraspecific variation of external characters (Figs 1B–H) such as body size,



Figure 3. Tergites and sternites of *Dysanabatium jacobsoni*. **A–C** female tergite VIII **D–F** female sternite VIII **G–H** female tergites IX–X. I male sternite VII **J–L** male tergite VIII **M–P** male sternite VIII. Scales: 0.5 mm.

coloration, punctation, the shapes of the head and pronotum. The sexual characters are somewhat variable, too, especially the shapes of the posterior margin of tergite VIII (Figs 3A–C, 3J–K) and sternite VIII (Figs 3D–F, 3M–P) in both sexes, and the shapes of the ventral process and the membranous structures of the aedeagus (Figs 4B–F). Specimens from Yunnan are usually relatively small (BL 4.83–6.04 mm, FL 2.95–3.45 mm), have blackish elytra (Figs 1C–D) sharply bicolorous femora, and partly (16 males and 9 females) a bright red pronotum (Fig. 1B). In the specimen from Guangxi the forebody has a faint blueish hue (Fig. 1E) and the sclerotized spine in the internal sac of the aedeagus is slender (Fig. 4D). All the specimens from Hainan have an on average larger body (BL 5.84–6.95 mm, FL 3.37–3.61 mm), a forebody with a weak or distinct metallic hue (Figs 1F–H), entirely black femora, and conspicuous membranous structures in the internal sac of the aedeagus (Figs 4E–F). In the material from Vietnam and Laos, most of the specimens have a black forebody, some have a more or less distinct blueish or greenish metallic hue, and



Figure 4. Aedeagus of *Dysanabatium jacobsoni*. **A** aedeagus in ventral view **B–F** aedeagus in lateral view (A–C Yunnan; **D** Guangxi; **E–F** Hainan). Scales: 0.5 mm.

seven specimens from Vietnam have a reddish pronotum. The legs of all the specimens from Vietnam and Laos are bicoloured, but the extent of the yellowish coloration of the femora is highly variable.



Figure 5. Habitat of Dysanabatium hainanense and D. jacobsoni in the Wuzhi Shan, Hainan.



Figure 6. Distribution of *Dysanabatium jacobsoni* in the Oriental and southern East Palaearctic regions (filled circles: examined records; open circles: records from Rougemont (1997)).

Distribution and natural history. According to Rougemont (1997), *D. jacobsoni* had been recorded from Indonesia (Java), Malaysia, Thailand, Vietnam, and one locality in the south of the Chinese province Yunnan. The currently known distribution is mapped in Fig. 6. The above specimens from Laos represent new country records. The altitudes of the examined material and of the material seen by Rougemont (1997) range from 200 to 1200 m. The specimens from China were found in flood debris, moss, leaf litter and soil near streams in evergreen broad leaved forest, partly together with *Dysanabatium hainanense* (Fig. 5).

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