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Molecular phylogeny of sea-skaters (*Halobates* Eschscholtz, 1822), relationship between Halobatini and Metrocorini, and a catalogue of the subfamily Halobatinae (Hemiptera: Heteroptera: Gerridae)

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Abstract
We investigated the phylogenetic relationships among seven of the ten Halobatinae genera (Heteroptera: Gerridae) based on COI+II, 16S rRNA, and 28S rRNA genes. Our analyses recovered monophyly of Halobatinae, and suggested paraphyly of Metrocorini caused by the position of *Ventidius* and *Esakia*. Since our phylogenies did not infer monophyly of the subgenus *Halobates* (s.str.) within Halobatini, we synonymized *Austrobates* and *Halobates* (*Hilliella*) with *Halobates*. We confirmed that (1) the limnic lifestyle of Metrocorini was ancestral in Halobatinae, (2) the marine lifestyle evolved only once in the common ancestor of *Asclepios* + *Halobates*, (3) the limnic lifestyle of some members of *Halobates* was independently derived from marine ancestors, and that (4) the open ocean was colonized at least three times in *Halobates*. A catalogue of Halobatinae organized according to an updated classification is presented, including all known geographic distributions, bibliographical references, and additional notes to all species of the subfamily.

Keywords
Gerridae; Halobatinae; molecular phylogeny; systematics; species catalogue

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Introduction

Members of the infraorder Gerromorpha (Insecta: Hemiptera: Heteroptera) are among the most ecologically diverse lineages of all semi-aquatic insects. Species in this clade have colonized the surface of all types of aquatic habitats on all continents except Antarctica (Andersen 1982). Eight gerromorphan families are currently recognized: Mesoveliidae, Hebridae, Hydrometridae, Hermatobatidae, Paraphrynoveliidae, Macroveliidae, Veliidae and Gerridae (Polhemus & Polhemus 2008), but the phylogenetic relationships within and among them remain a matter of debate (Damgaard 2012).

Gerromorphan bugs, which probably diverged from terrestrial forms inhabiting the hygropetric zone along lentic and lotic habitats, have adapted to live on the surface of water in multiple ways. The variety of adaptations used to deal with different ecological and environmental conditions experienced across their habitats have caused Gerromorpha to become the focus of multiple investigations on their evolution, ecology and behavior (Spence & Andersen 1994). This is especially true for representatives in the gerrid subfamily Gerrinae, which includes the well-known water striders or pond skaters from north temperate regions (*Gerris* Fabricius, 1794; *Aquarius* Schellenberg, 1800; *Limnoporus* Stål, 1868). Studies on these three principal Holarctic genera have led to generalizations that are frequently applied to the entire family or even the entire infraorder (Andersen & Weir 1994a; Chen *et al.* 2005; Ye *et al.* 2018).

In tropical regions, despite the fact that taxonomic and ecological diversity of gerromorphan bugs is much higher, research is still largely focused on classical taxonomy and geographic distributions of species, with only few studies on their natural history. One notable exception are members of Halobatinae which have attracted considerable attention from researchers. Most species of Halobatinae, found in lotic freshwater habitats in the Old World tropics (Andersen 1982; Chen *et al.* 2005), but a considerable number of species have invaded marine environments (estuaries, lagoons and mangroves) and five species have even adapted to a life on the open oceans, which is unparalleled among insects (Andersen & Cheng 2004; Cheng *et al.* 2012).

In this study we present an in-depth review on Halobatinae phylogeny and evolution based on studies from Andersen (1991) and Damgaard *et al.* (2000), and expand the taxonomic sampling to include seven of the ten recognized genera of Halobatinae. Furthermore, we provide an updated catalogue containing all described species of the subfamily, their known geographic distributions, bibliographical references, and additional notes (see Appendix 1).

Historical perspective on Halobatinae ecological evolution

China (1955) was the first to suggest a single transition from limnic to marine habitats in the subfamily Halobatinae. Later, Matsuda (1960) subdivided the Halobatinae into two tribes: (i) Metrocorini, including a number of freshwater taxa from the Oriental and Afrotropical regions, and (ii) Halobatini, comprising marine taxa from the Indo-Pacific (Andersen 1982; Chen *et al.* 2005). Although this separation was primarily based on ecological preferences, Matsuda, who also analyzed several diagnostic

morphological features, suggested that species of Metrocorini have their metasternum reduced to a triangular plate and are often wing-dimorphic, while the metasternum in Halobatini extend to the metacetabular region laterally, and members of this tribe are always apterous. Based on these differences, Matsuda hypothesized the sister-group relationship between *Halobates* Eschscholtz, 1822 and *Asclepios* Distant, 1915 within Halobatini, and proposed a clade comprising the Oriental genus *Metrocoris* Mayr, 1865 as sister group to an unresolved trichotomy comprising three Afrotropical genera (*Eurymetra* Esaki, 1926, *Eurymetropsis* Poisson, 1948, and *Eurymetropsiella* Poisson, 1950), and another clade comprising the Afrotropical genus *Eurymetropsielloides* Poisson, 1956 as sister group to two Oriental genera (*Esakia* Lundblad 1933, and *Ventidius* Distant, 1910, including the subgenus *Ventidioides* Hungerford & Matsuda, 1960). Subsequent studies on Metrocorini included the description of a new genus, *Ventidiopsis* Miyamoto, 1967 (now subgenus of *Ventidius*), and revisions and descriptions of species in *Ventidius* (Cheng 1965, 1966; Chen & Zettel 1999; Lansbury 1990), *Metrocoris* (Chen & Nieser 1993a, 1993b; Chen 1994) and *Esakia* (Cheng 1966).

While our present knowledge on Metrocorini is still largely based on traditional classification with little understanding of phylogenetic relationships among species and genera, members of Halobatini have been the focus of several phylogenetic studies. Distant (1915) established the genus *Asclepios* for *A. annandalei* Distant, 1915, and China (1957) erected the subgenus *Hilliella* China, 1957 for *Halobates mjobergi* Hale, 1925 and suggested that the marine environment had been colonized only once by the most recent common ancestor of *Aclespios* and *Halobates*. Herring (1961) expanded these studies by dividing *Halobates* into several presumably monophyletic species groups, and suggested that transition from a coastal to a pelagic lifestyle had occurred only once in this genus (i.e. *H. micans* group). The *Halobates* species groups proposed by Herring (1961) were later tested by Andersen (1991) using cladistics analyses on a morphological dataset predominantly based on male terminalia. This study re-organized the species groups according to a new phylogenetic hypothesis. More recently, Cheng (2008) updated the species groups of Andersen (1991) by including new evidence from Andersen & Weir (1994) and Andersen & Cheng (2004). Even though two species of *Halobates* have been described from freshwater habitats in Australia (*Halobates* (s.str.) *acherontis* J. T. Polhemus, 1982, collected 100 km upstream of Daly River in Northern Territory (J. T. Polhemus, 1982), and *H.* (*Hilliella*) *robinsoni* Andersen & Weir, 2003 from the Robinson River, Western Australia (Andersen & Weir 2003)), they were considered occasional migrants or secondary reversals to the limnic environment. However, with the discovery of *Austrobates rivularis* Andersen & Weir, 1994 from freshwater creeks in northern Queensland, apparentely an intermediate-form between *Asclepios* and *Halobates* but with stronger affinities to the latter, discussions about the origin of marine lifestyle in Halobatini were fully revitalized. It was speculated that ancestral Halobatini had been euryhaline, with *Asclepios* developing a preference for marine habitats, and *Austrobates* and *Halobates* evolving respectively into species preferring limnic or marine habitats (Andersen 1991; Andersen & Weir 1994b). Furthermore, although the only fossil Halobatini was discovered in Italy (Andersen *et al.* 1994), Andersen (1998) concluded that the Indo-Malayan archipelago

Table 1. Total number of known species in each genus or subgenus, and number of species sequenced for this study. Species numbers in Halobatini according to the previous taxonomy.

Tribe	Genus or subgenus	Total species described	Species sequenced
Halobatini	*Asclepios*	3	3
	Austrobates	1	1
	Halobates	48	22
Metrocorini	*Esakia*	10	1
	Eurymetra	7	2
	Eurymetropsiella	3	0
	Eurymetropsielloides	1	0
	Eurymetropsis	2	0
	Metrocoris	80	4
	Ventidius (*Ventidius*)	12	2
	Ventidius (*Ventidioides*)	9	0
	Ventidius (*Ventidiopsis*)	2	1

was the ancestral home of various lineages of Halobatini based on extant distributions of *Austrobates* and *Halobates* (*Hilliella*) in Australia and *Asclepios* in South and South-East Asia.

While Andersen (1991) established an excellent basis for testing hypotheses on taxonomy, phylogeny, adaptation, and evolution of Halobatinae, he realized that his interpretation of primitive and derived character states was problematic due to rapid evolution of the male terminalia and ecological constraints associated with a marine lifestyle. Therefore, a maximum parsimony analysis was carried out by Damgaard *et al.* (2000) using both a modified version of the morphological data matrix from Andersen (1991) and a new set of DNA sequence data from the mitochondrial gene encoding *cytochrome oxidase subunit I* (COI). The resulting topology largely agreed with Andersen (1991), but revealed considerable incongruence between molecular data and morphology at the deeper nodes (e.g. parsimony analysis of the molecular data showed both *Austrobates* and *Halobates* (*Hilliella*) deeply nested within *Halobates* s. str.).

While phylogenetic relationships among oceanic *Halobates* species have been addressed in subsequent studies (Andersen *et al.* 2000; Leo *et al.* 2012), little has been done to further investigate the deeper relationships among various genera of Halobatinae. Among the exceptions is the study by Damgaard (2008) primarily based on a morphological data set derived from Andersen & Weir (2004b) and DNA sequence data for COI+II, 16S rRNA and 28S rRNA. Although only limited taxa were available for the study, he found Halobatini (two species of *Halobates* and one species of *Asclepios*) nested within Metrocorini (one species each of *Metrocoris* and *Ventidius*). We were able to obtain a greatly expanded taxa sample for the present study (Table 1).

Materials and methods

Samples from seven genera including species from various locations over the world were available for this study. Unfortunately, we were unable to obtain samples of the

African and Madagascan endemics *Eurymetropsiella, Eurymetropsielloides,* and *Eurymetropsis*. The total number of described species for each genus and the number available for DNA sequence are shown in Table 1. We expanded DNA sequence data to 2,268 bp from four genes encoding COI+II, 16S rRNA and 28S rRNA following previous studies by Damgaard *et al.* (2000) and Damgaard (2008).

We selected one species each from Ptilomerinae (Gerridae) and Haloveliinae (Veliidae) as outgroups. *Ptilomera* Amyot & Serville, 1843 (Ptilomerinae) was chosen as a close outgroup because Ptilomerinae and Halobatinae were hypothesized to be a sister group to all other subfamilies of Gerridae (Andersen 1982; Damgaard 2008). *Halovelia* Bergroth, 1893 (Haloveliinae) was chosen as a more distant outgroup. The clade Haloveliinae + Microveliinae, currently included in the paraphyletic Veliidae, was recovered as sister to the Gerridae by Damgaard (2008).

Molecular data collection

Table 2 lists all the samples analyzed in this study with collecting data, references, and GenBank accession numbers. Total genomic DNA was extracted from ethanol preserved specimens following the QIAGEN DNEasy Purification Kit Protocol (Qiagen Inc., Santa Clara, California), except for the final elution, which was done twice in 200 µl EB buffer using a single centrifugation step. All PCR amplifications took place in a cocktail of 2 µl DNA template, 20 µl GATC mix (0.02 mM of each nucleotide), 14 µl ddH_2O, 5 µl Amplicon III 10x key buffer (15 mM $MgCl_2$) (VWR International, West Chester, Pennsylvania), 5µl of each of the sense and anti-sense primers and 0.2 µl Amplicon III *Taq* polymerase (VWR International, West Chester, Pennsylvania). In case of no amplification, 5 µl of ddH_2O was replaced by 5 µl Amplicon III 10x standard buffer (15 mM $MgCl_2$) (VWR International, West Chester, Pennsylvania). The PCR amplifications were performed under the following conditions: 10 min at 94°C (hot start) followed by 25–30 cycles of 45 seconds at 94°C (denaturing), 45 seconds at 45–48°C (annealing), and 60 seconds at 72°C (extension). PCR-amplicon electrophoresis was done on a 2% low melting agarose gel and stained with SYBR® (Invitrogen, Eugene, Oregon) under UV-light. Positive amplicons were purified using QIAQUICK PCR Purification Kit (Qiagen Inc., Santa Clara, California) and sequenced using the ABI Sequencing Reaction Kit (Applied Biosystems, Foster City, California). Sequencing products were purified using QUIAGEN DyeEx 2.0 Spin Kit (Qiagen Inc., Santa Clara, California) and ran on ABI 3130xl Analyzer (Applied Biosystems, Foster City, California). All vouchers and DNA extractions were stored at the Natural History Museum of Denmark. Table 3 lists primers used in this study. A number of internal primers were designed in order to amplify and sequence overlapping fragments of COI+II for the many deviant taxa.

Phylogenetic analyses

Sequence editing and contig construction for each segment was performed in Sequencher 4.10 (Gene Codes Corporation Inc., Ann Arbor, Michigan). PAUP* b4.08 (Swofford 1998) was used for assembling and aligning the combined sequences

Table 2. Sample information and accession number of species included in the study. GB = Genbank database, Ext = reference (isolate) number. Sequences primarily from Damgaard et al. (2000), Damgaard (2008), and Muraji & Tachikawa (2000). *Halobates* species groups after Cheng (2008).

Taxon	Collecting site	Year	Collector	Ext.	COI+COII	16S rRNA	28S rRNA
Eurymetra							
E. natalensis	Tanzania, Usa River E of Arusha	1997	P. Gravlund	10jd4	AF200281	--------	--------
E. natalensis	South Africa, Kwazulu-Natal	2007	J. Pedersen	1724	KY315652	KU366411	KU366457
E. madagascariensis	Madagascar, Monte des Francais	2007	E. Guilbert	1957	KY315654	KU366410	KU366458
Metrocoris							
M. strictus	Thailand, Chiang Rai	1996	M. Andersen	57	EU871340	EU871205	EU871266
M. esakii	Japan, Okinawa	1995	GB	--------	--------	AB026604	AB034777
M. histrio	Japan, Honshu	1995	GB	--------	--------	AB026603	AB034780
M. luzonicus	Philippines, Laguna, Los Baños	1995	GB	--------	--------	AB026605	AB034779
Metrocoris sp.					AY252971	AY252704	AY252475
M. tenuicornis	Malaysia, Sarawak, Lipad river	2000		1020	KY315649	KU366415	KU366428
M. stranguloides	Laos, Vientiane Province	2008	J. Pedersen	2107	KY315656	KU366415	KU366427
M. nigrofasciatus group	India, Arunachal Pradesh	2008	M. Fikacek	2207	KY315658	KU366412	KU366425
Esakia							
Esakia sp.	Malaysia, Tabin W.R., Lipad River	2000		1019	KY315648	KU366409	KU366429
Ventidius							
V. longitarsus	Laos, Champasak Province	2008	J. Pedersen	2126	KY315657	KU366373	KU366418
V. usingeri	Philippines, Polillo, Panuculan	2004	H. Zettel	1059	EU871341	EU871207	EU871268
V. yangae	Malaysia, Tabin W.R., Lipad River	2000		1018	KY315647	KU366375	KU366424

Aslepios							
A. annandalei	Singapore, Pulau Ubin	1997	KL. Yeo	H169	KY315681	EU871206	EU871267
A. annandalei	India, South Andaman	2008	N. F. Munch-Petersen	1982	KY315655	KU366406	KU366420
A. shiranui	Japan, Kyushu	1998	GB	--------	--------	AB026606	AB034775
A. shiranui	Japan, Kyushu, Nagasaki	2008	T. Ikawa	2630	KY315661	KU366407	KU366459
A. apicalis	Vietnam, Hoi An River	2006	N. F. Munch-Petersen	1451	KY315651	KU366408	KU366422
Austrobates							
A. rivularis	Australia, QLD, Lydia Creek	1993	P. Zborowski	52	KY315643	KU366384	KU366453
A. rivularis	Australia, QLD, Andoom Creek	1994	P. Zborowski	103	KY315664	KU366383	KU366452
***Halobates* (*Hiliella*)**							
H. mjobergi	Australia, QLD, Roonga Point	1992	T. Weir/P. Zborowski	H72b	KY315669	AY648134	AY648150
Halobates s.str. regalis gr.							
H. darwini	Australia, WA, Kimberley Coast	2006	R. Pitman	2423	KY315660	KU366460	---------
H. peronis	Papua New Guinea	1990	L. Cheng	H176	KY315684	KU366404	KU366450
H. sexualis	Sri Lanka, Beruwela	1995	M. Nummelin	H177	KY315685	KU366402	KU366449
H. whiteleggei	Australia, NSW, Durras Lake	1994	E.S. Nielsen	H179	KY315687	KU366376	KU366430
alluaudi gr.							
H. alluaudi	Seychelles, Daros Is.	1990	R/V Gitte Gry	H79	KY315673	KU366394	KU366455
H. alluaudi				H111	KY315680	KU366393	KU366456

(Continued)

Table 2. Sample information and accession number of species included in the study. GB = Genbank database, Ext = reference (isolate) number. Sequences primarily from Damgaard et al. (2000), Damgaard (2008), and Muraji & Tachikawa (2000). *Halobates* species groups after Cheng (2008). (*Cont.*)

Taxon	Collecting site	Year	Collector	Ext.	COI+COII	16S rRNA	28S rRNA
robustus gr.							
H. robustus	Galapagos Is., Cartago Bay	1982	P. Holdway	H99	KY315676	KU366395	KU366445
poseidon gr.							
H. poseidon	Indian Ocean, Cosmoledo Atoll	1989	D.A. Polhemus	H78	KY315672	KU366388	KU366446
mariannarum gr.							
H. katherinae	New Caledonia	2001		422	KY315645	KU366387	KU366444
H. mariannarum	Caroline Is., Pohnpei		R. Reame	H53	KY315667	KU366386	KU366447
H. fijiensis	Fiji, Suva Coast	1986	R. Hauser	H173	KY315682	KU366385	KU366443
matsumurai gr.							
H. nereis	W. Caroline Is., Palau	1995	L. Cheng	H103	KY315679	KU366396	KU366441
H. matsumurai	Japan, Imari, Saga	1998	GB		---------	AB026607	AB034778
H. matsumurai	Japan, Kyushu, Nagasaki	2008	T. Ikawa	2632	KY315663	KU366397	KU366419
bryani gr.							
H. bryani	Fiji, Suva Estuary	1986	R. Hauser	H178	KY315686	KU366399	KU366442
hayanus gr.							
H. hayanus	Papua New Guinea	1990	L. Cheng	H175	KY315683	KU366389	KU366437
H. calyptus	Sulawesi, Bangka Is.,	2003	L. Cheng	2388	KY315659	KU366390	KU366439
micans gr.							
H. flaviventris	Seychelles, Daros Is.	1990	R/V Gitte Gry	H76	KY315671	KU366379	KU366440
H. flaviventris				H83	KY315674	KU366382	KU366435
H. germanus	Arabian Sea	1995	M. Baars	H29	KY315666	KU366392	KU366438
H. hawaiiensis	Society Is., Moorea	1996	V. Resh	H87	KY315675	KU366381	KU366434
H. micans	Arabian Sea	1995	M. Baars	H12	EU871339	EU871204	EU871265

H. micans	Mexican Gulf			H172			
H. sericeus	Central Pacific	1995	T. Villareal	H101	KY315677	KU366391	KU366436
H. sericeus	Japan, Honshu	1995	GB	--------	AB026608	AB034776	
H. sobrinus	Eastern Pacific	1982	P. Holdway	H57	KY315668	KU366380	KU366454
H. splendens	Eastern Pacific	1982	P. Holdway	H102	KY315678	KU366431	KU366431
proavus gr.							
H. proavus	Thailand, Phuket	1987	N. M. Andersen	H73	KY315670	KU366432	KU366432
japonicus gr.							
H. japonicus	Japan, Ishigakijima, Kabira Bay	2006	T. Ikawa	2631	KY315662	KU366398	KU366448
OUTGROUP							
Halovelia sp.	Iran, Sirik Mangrove Forest	2007	M. Mokhtari	1950	EU871302	EU871176	EU871236
Ptilomera kirkaldyi	Malaysia, Tabin W.R., Lipad River	2000	?	1016	EU871336	EU871201	EU871262

Table 3. Primers used in the present study for amplifying gene regions of 28S, 12S and COI+II.

Gene	Primer	Sequence	Reference
28S rRNA	28SL	5′CCCGTCTTGAAACACGGACCAA 3′	Muraji & Tachikawa 2000
	28SH	5′CCACAGCGCCAGTTCTGCTTAC 3′	Muraji & Tachikawa 2000
16S rRNA	16sA	5′CGCCTGTTTAACAAAAACAT 3′	Cognato & Vogler 2001
	16sB2	5′ TTTAATCCAACATCGAGG 3′	Cognato & Vogler 2001
COI+II	C1-J-1751	5′ GGATCACCTGATATAGCATTCCC 3′	Simon *et al.* 1994
	C1-N-2191	5′ CCCGGTAAAATTAAAATATAAACTTC 3′	Simon *et al.* 1994
	C1-J-2183	5′CAACATTTATTTTGATTTTTTGG3′	Simon *et al.* 1994
	TL-2-3014	5′TCCAATGCACTAATCTGCCATATTA 3′	Simon *et al.* 1994
	C1-J-2798	5′CCWCGWCGWTAYTCWGAYTATCC 3′	Damgaard & Cognato 2006
	C1-N-3389	5′CCACAAATTTCTGAACATTGACCA 3′	Simon *et al.* 1994
	C2-N-3554	5′ GTTCATGARTGWARCACATC 3′	Damgaard & Cognato 2006

manually in combination with ClustalX (Thompson *et al.* 1997) using default parameters. Combined parsimony analyses were performed in PAUP* using 100 random taxon-addition replicates, and with gaps scored as a fifth character. Branch support measurements were evaluated by bootstrap analyses (Felsenstein 1985) using 500 simple taxon addition pseudoreplicates and by Bremer support (BS; Bremer 1994) using constrained files generated in TreeRot v.2a (Sorensen 1999), and ran in PAUP* with all other parameters set as defaults.

Bayesian analyses were performed in MrBayes 3.2 (Huelsenbeck & Ronquist 2001; Ronquist *et al.* 2012) using six different partition schemes for the superalignment (COI+II, 16S rRNA, and 28S rRNA). This approach accounts for (i) (potential) differences in phylogenetic signal among genes in the superalignment (Huelsenbeck & Bull 1996), (ii) differential substitution rates across positions in protein encoding genes (Springer *et al.* 2001), (iii) distinction between nuclear and mitochondrial genomes (Moore 1995), and (iv) structural constraints that affect the non-protein coding genes (Lescoute *et al.* 2005).

Partitioning schemes were compared using Bayes factors (BF hereafter): – partitioning #1: non partitioned super-alignment (COI+II + 16S rRNA + 28S rRNA); partitioning #2: partitioned by each gene (COI+II, 16S rRNA and 28S rRNA); partitioning #3: partitioned by gene and by codon within COI+II (COI+II [1st position], COI+II [2nd position], COI+II [3rd position], 16S rRNA and 28S rRNA); partitioning #4: two partitions specified by first and second codon positions of COI+II (COI+II [1st position] + COI+II [2nd position]) and the second one including the third position of COI and both ribosomal genes (COI+II [3rd position] + 16S rRNA + 28S rRNA); partitioning #5: because concordant phylogenetic signal was found between the ribosomal genes, 16S rRNA and 28S rRNA were analyzed in a partition and COI+II independently (COI+II and 16S rRNA + 28S rRNA); and partitioning #6: partitioned by gene including only the mitochondrial loci (COI+II and 16S rRNA). Results using

partitioning strategy #4 with the better fit in comparison to all other schemes (i.e. BF > 10) are presented here.

We used the general time reversible substitutional model (Yang 1994) with invariable sites and gamma distribution for each partition (GTR+I+G). This model was selected in jModelTest (Posada 2008) based on BIC criteria. We set unlinked partition-specific substitution rates (*revmat*), gamma shapes (*shape*), character state frequencies (*statefreq*), transition/transversion rate ratios (*tratio*), proportion of invariable sites (*pinvar*) and partition specific rates (*ratepr* = *variable*). We estimated the minimum run length to reach a stationary state based on preliminary analyses (0.5–50 × 10^6 MCMC generations). The final run for each dataset consisted of 50 × 10^6 iterations with parameters logged every 50 × 10^3 samples. The convergence of MCMC runs was assessed by considering estimated sample size (ESS) above 200 in Tracer 1.4 (Rambaut & Drummond 2007). All analyses were based on a post-burning fraction consisting of 75% of the generations. The consensus tree was constructed specifying a 50% majority rule. Two independent Bayesian analyses were performed by selecting 16 total chains (i.e. 8 per run) as implemented in MrBayes on the CIPRES cluster (Miller *et al.* 2011).

We used RAxMLGUI 1.5 (Silvestro & Michalak 2012) for maximum likelihood (ML) analyses. In RAxML analyses, the superalignment was partitioned in accordance to the best scheme (i.e. partitioning scheme #4, see above). We selected 10 independent runs (–N 10) and used a GTRGAMMA model with 10,000 replicates to estimate bootstrap support.

Results

Data sets

The primers for 16S rRNA and 28S rRNA worked well for most samples. Only a few specimens failed to amplify and sequence these genes. The protein coding genes COI+II, on the other hand, were more problematic due to numerous base substitutions (especially in third codon positions) and a number of specimens failed to amplify and sequence the entire segment. The assembled and aligned data set consisted of 2,376 characters, of which 1,374 characters came from COI+II, 442 characters from 16S rRNA and 560 characters from 28S rRNA. All sequences are available from GenBank (see Table 2 for accession numbers).

Phylogenetic relationships

Parsimony (Fig. 1), maximum likelihood (Fig. 2), and Bayesian inference (Fig. 3) phylogenies generated congruent and well-resolved systematic hypothesis. Phylogenetic reconstruction based on parsimony indicated a strict consensus of three equally parsimonious trees, each with 4,101 steps (CI = 0.3192; RI = 0.4909; Fig. 1). From the 2,376 characters analyzed, 1,507 were invariable, 636 were considered phylogenetically informative, and 233 were autapomorphic. Table 3 summarizes bootstrap values (bst hereafter) from parsimony majority-rule consensus trees and maximum likelihood

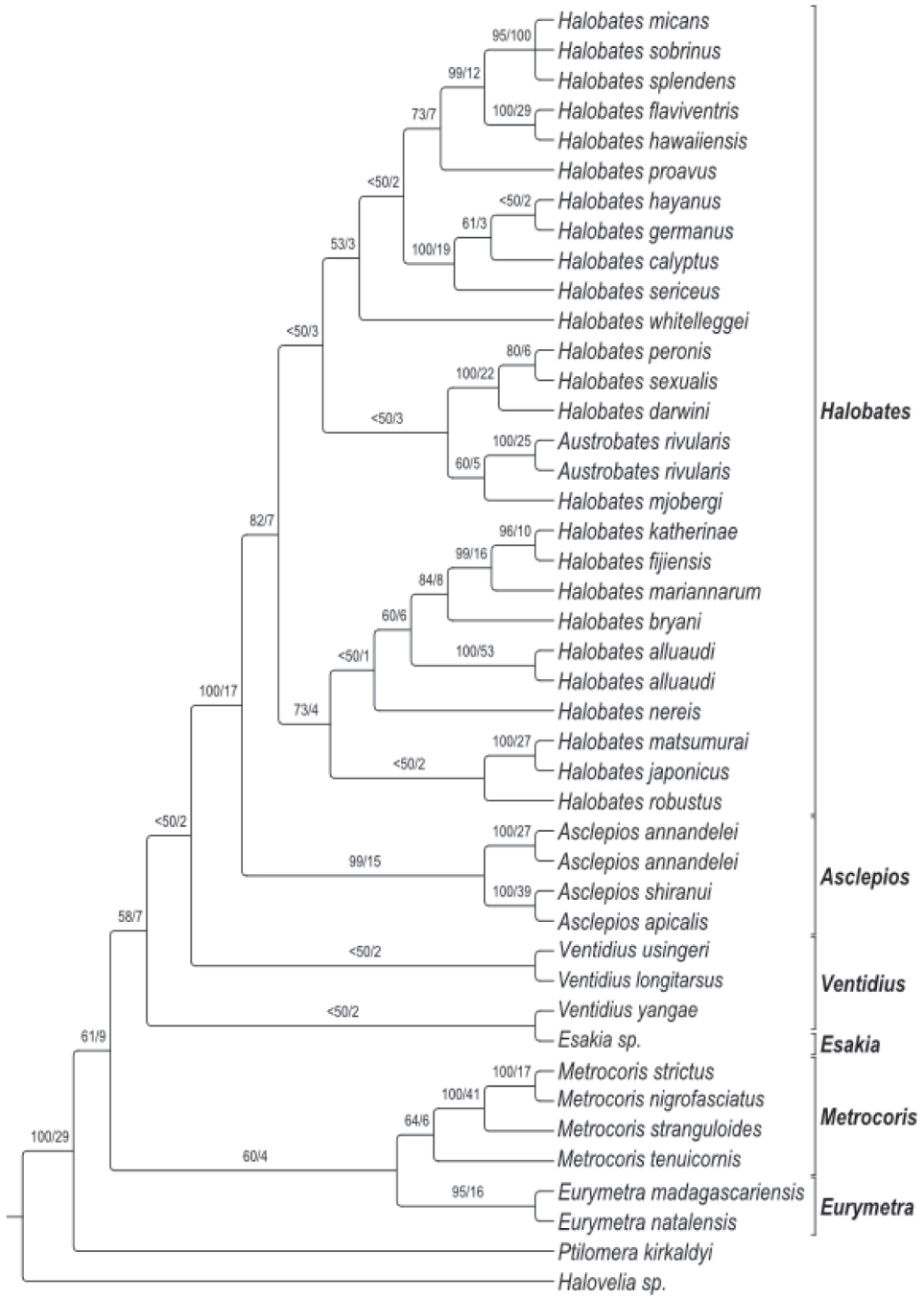

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Fig. 1. Strict consensus of three equally parsimonious trees resulting from a phylogenetic analysis of all data with gaps scored as a fifth character state. Numbers above branches refer to bootstrap support values and Bremer support (separated by/). Species are labeled using the previous classification. However, generic delimitation followed in the current paper is presented in the right side of the tree (see Tables 4 and 5).

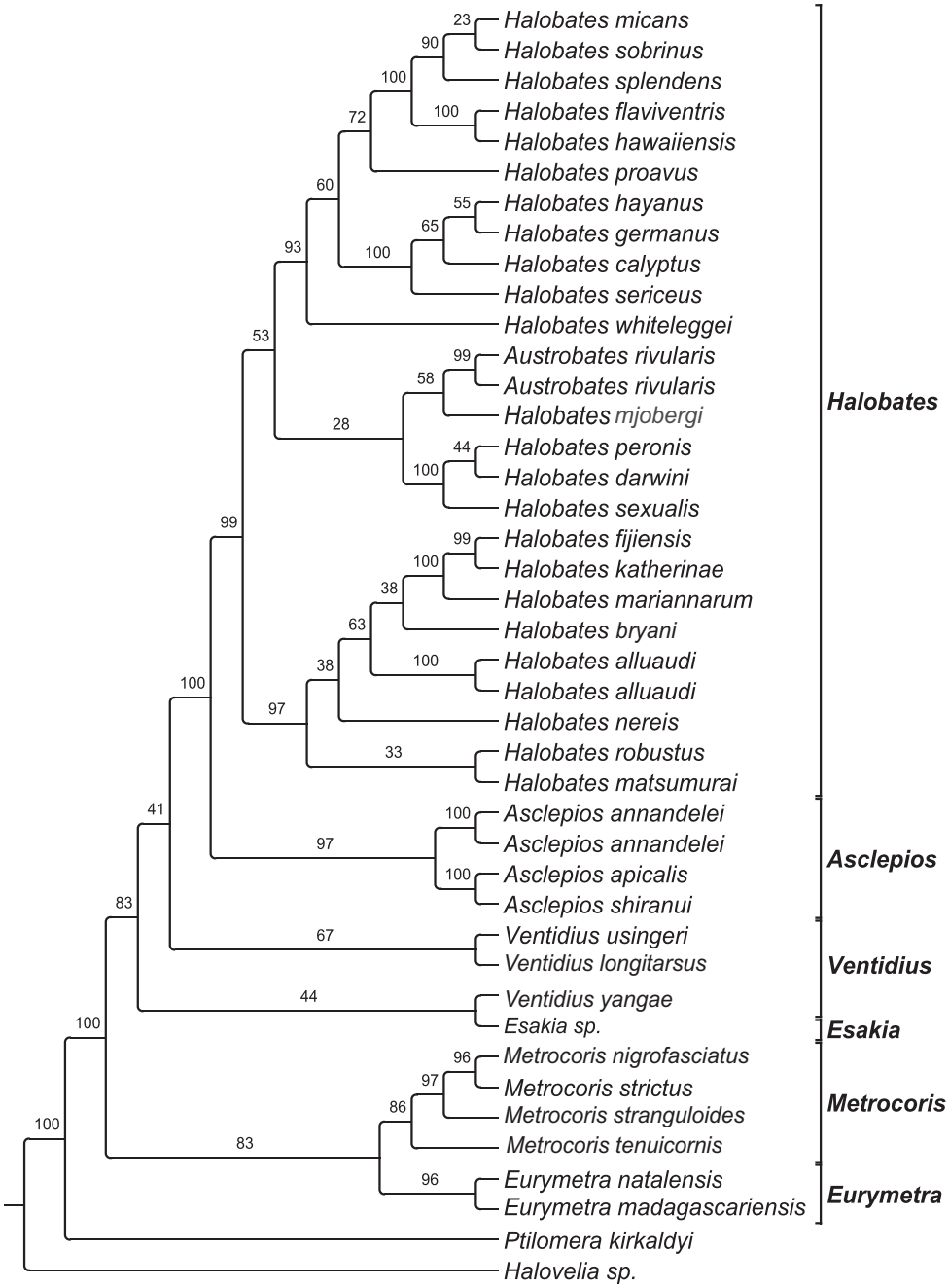

Fig. 2. Maximum likelihood reconstruction of phylogenetic relationships within Halobatinae. Likelihood = –20,809.9759, with clade bootstrap supports above branches. Species are labeled using the previous classification. However, generic delimitation followed in the current paper is presented in the right side of the tree (see Tables 4 and 5).

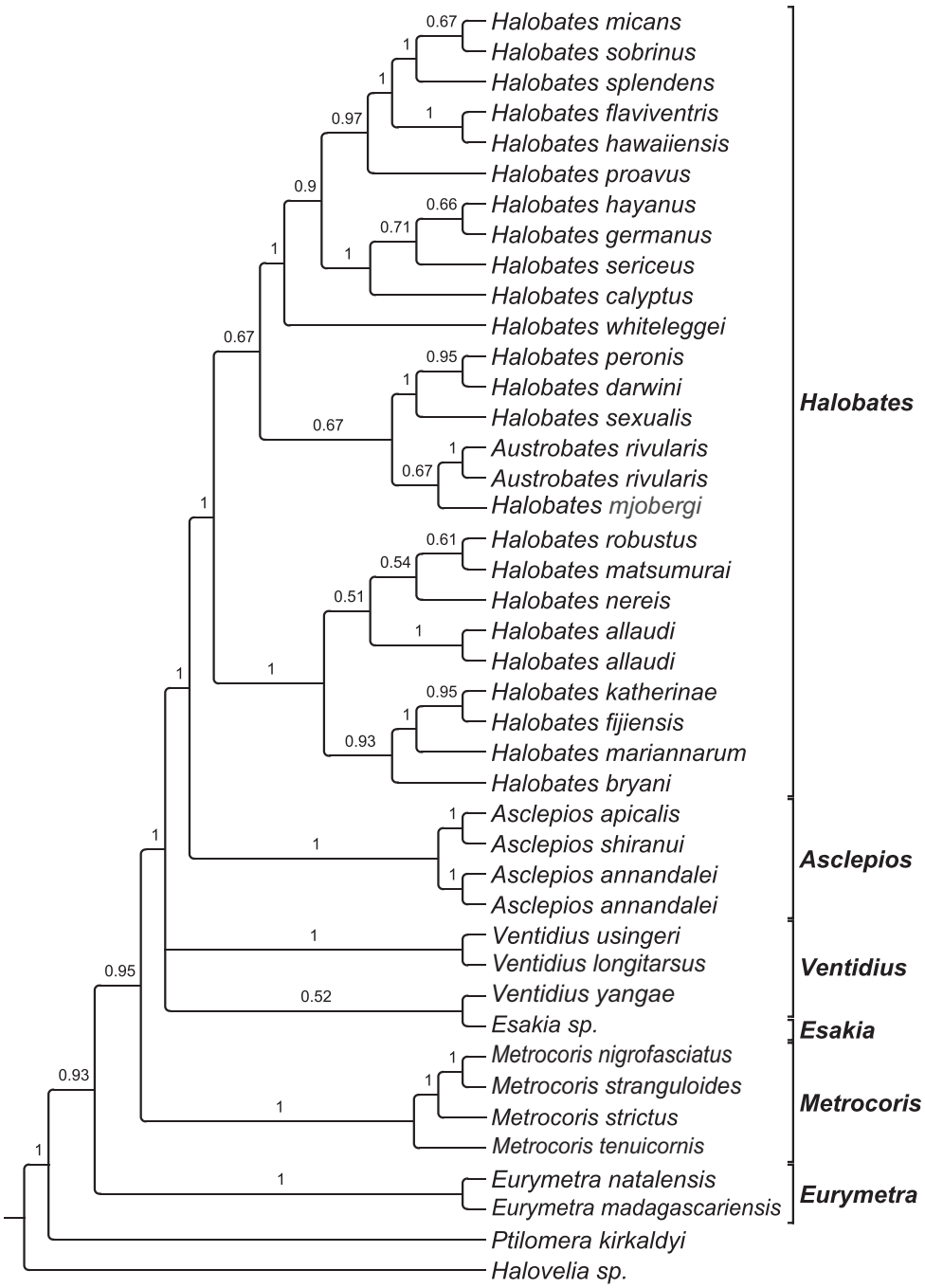

Fig. 3. Maximum clade credibility tree for the phylogenetic analysis of Halobatinae based on COI+II, 12s, 16s and 28s loci. Posterior probabilities indicated above branches for each clade. Species are labeled using the previous classification. However, generic delimitation followed in the current paper is presented in the right side of the tree (see Tables 4 and 5).

Table 4. Support values for different clades of Halobatinae based on the updated classification of the subfamily. Here we summarize four different measurements derived from three methods for inferring phylogenetic relationships.

Clade	Parsimony		Likelihood	Bayesian
	Bootstrap	Bremer Support	Bootstrap	Posterior Probability
Halobatinae	61	9	100	1
Halobatini	100	17	100	1
Halobates	82	7	99	1
Asclepios	99	15	97	1
Ventidius[a]	-	-	-	-
Esakia[b]	-	-	-	-
Metrocorini[a]	-	-	-	-
Eurymetra	95	16	96	1
Metrocoris	64	4	86	1

[a] Paraphyletic or polyphyletic lineage.
[b] Represented by a single sample.

analyses, Bremer supports, and posterior probabilities (pp hereafter) for clade support. Regardless of the phylogenetic method employed, the overall phylogenetic pattern is highly supported and conserved within Halobatinae.

Subfamily monophyly was recovered by molecular data (61 MP-bst; 100% ML-bst; 1 pp; Figs 2–4). The monophyly of Halobatini in the current sense (= *Asclepios* + *Halobates*) was highly supported by parsimony-likelihood bootstrap (100% and 100%, respectively; Table 4) and posterior probability (1 pp). Relationships within the tribe were fully resolved and supported at the generic level, with *Asclepios* being highly supported as the sister clade of *Halobates* (99% MP-bst; 97% ML-bst; 1 pp). The Systematic position of *Austrobates* within *Halobates* s.str. was indicated by all analyses (99% ML-bst; 100% MP-bst; 1 pp), contradicting its systematic validity as a different genus. *Halobates* (*Hilliella*) was recovered by all analyses as the sister clade of *Austrobates* (60% MP-bst; 58% ML-bst; 0.67 pp; Figs 2–4).

Our phylogenetic reconstructions suggested paraphyly of Metrocorini derived from the positions of *Ventidius* (polyphyletic; <50% MP-bst; 67% ML-bst; 0.99 pp) and *Esakia* (<50% MP-bst; 44% ML-bst; 0.51 pp) being closer to *Asclepios* and *Halobates* than to *Eurymetra* and *Metrocoris*. The analyses also recovered a monophyletic clade composed of *Metrocoris* + *Eurymetra* (60% MP-bst; 53% ML-bst; 0.99 pp), but the small sample available for these genera limits our conclusions. The paraphyly of *Ventidius* was recovered in all our phylogenies and was caused by *Ventidius yangae* Chen & Zettel, 1999 being closely related to *Esakia* (<50% MP-bst; 44% ML-bst; 0.52 pp). Based on these results, we suggest that (1) *Ventidius* s. str. shares its most recent common ancestor with Halobatini in the current sense, and that (2) *Ventidius* subgenus *Ventidiopsis* is more closely related to *Esakia* than *Ventidius* s. str.

Discussion

The phylogenetic relationships within Halobatinae have been a matter of debate and are still poorly resolved (see Damgaard 2012). Previous studies have supported Halobatini monophyly and indicated paraphyly of Metrocorini (e.g. Damgaard 2008). However, both the limited sampling and conflicting signals between morphology and molecular datasets have presented uncertainties of these hypothesized phylogenetic relationships. We provide here the most comprehensive species-level molecular phylogeny published so far for the entire subfamily. However, we acknowledge that the species sampling for freshwater genera is scarce in our tree, and further studies should focus on addressing this aspect. Our analyses recovered the monophyly of Halobatinae, but suggested paraphyly for Metrocorini (see also Damgaard 2008). We also update the taxonomic classification for Halobatinae based on recovered phylogenetic relationships. The highlights of this new taxonomic arrangement include recovery of monophyly of Halobatini, paraphyly of Metrocorini, as well as support for the monophyletic status of *Halobates*. Discussions on several aspects related to taxonomy, phylogeny, ecology, and biogeography of the subfamily are given below.

Taxonomic status of Metrocorini and Halobatini

Matsuda (1960) established the tribe Halobatini for the marine genera *Halobates* and *Asclepios*, and Metrocorini for all limnic genera. We found Metrocorini is less convincingly defined in our study compared to Halobatini; its monophyly has also been questioned by Muraji & Tachikawa (2000) and more recently by Damgaard (2008). Based on available genera sampled our results show that *Esakia* and *Ventidius* are in fact more closely related to *Asclepios* + *Halobates* and should therefore be included in the Halobatini, whereas Metrocorini should include *Metrocoris* + *Eurymetra*. However, given our limited sampling within Metrocorini, we do not attempt to make any formal taxonomic proposal regarding this tribe at present.

We would like to emphasize that the genus *Eurymetra,* which in our phylogenetic analyses represents the sister clade of *Metrocoris*, is morphologically more similar to *Eurymetropsiella* and *Eurymetropsis* (both unavailable for our study; see Matsuda 1960). This tentatively supports the current position of *Eurymetropsiella* and *Eurymetropsis* within Metrocorini. Future studies, when samples become available, should be focused on addressing the phylogenetic relationships within Metrocorini and the position of these three genera within the Halobatinae phylogeny.

Taxonomic status of Halobates *subgenus* Hilliella

China (1957) erected the subgenus *Hilliella* for *H. mjobergi* (type species) and *H. apicalis* Esaki, 1924. Characters used to support this subgenus were (i) absence of a hair fringe on the first segment of the middle tarsus, (ii) pale strips on the fore and middle femora and tibiae, and (iii) hairy processes of the eighth abdominal segment in the male. More recently, J. T. Polhemus & Cheng (1982) placed *H. zephyrus* Herring,

1961 in *Hilliella* because of its hypothetical relationship to *H. mjobergi*. This was refuted by Andersen (1991) who placed it in the *H. regalis* group and synonymized *Hilliella* with *Halobates*. However, Andersen & Weir (1994b) re-established *Hilliella* to include *H. mjobergi* and their newly discovered *H. lannae* Andersen & Weir, 1994, and later added *H. robinsoni* to this subgenus (Andersen & Weir 2003).

Morphological characters suggested by China (1957) to support the subgeneric status for *H.* (*Hilliella*) *mjobergi*, could be considered specific apomorphies as pointed out by Andersen (1991). This is supported by molecular evidence presented here that points out the systematic inconsistency of the subgenus *H.* (*Hilliella*). Although only the type species *H.* (*Hilliella*) *mjobergi* was available for the present study, we found it deeply nested within *Halobates* s. str., suggesting that the two subgenera should be synonymized. This proposal aims to minimize the number of non-monophyletic lineages within Halobatinae. Since the clade *Austrobates* + *Hilliela* had always been treated as a sister clade to *H. darwini* Herring, 1961, *H. sexualis* Distant, 1903, and *H. peronis* Herring, 1961, we prioritized monophyly of *Halobates* s. str. by avoiding the establishment of subgeneric categories within *Halobates.* Similar consideration was extended to *Austrobates* below.

Taxonomic status of Austrobates

When Andersen (1991) published the first cladistic analysis of *Asclepios* and *Halobates*, he used a dataset with 64 characters and 30 taxa (including two species of *Asclepios* and 27 species of *Halobates*). When describing *Austrobates rivularis*, Andersen & Weir (1994a) scored the species for the same characters used in Andersen (1991) and found that *Austrobates* assumed a position as sister group to *Halobates* s.l. in all the most parsimonious trees. More recently, Damgaard *et al.* (2000) reanalyzed the data set from Andersen (1991) for selected taxa with the addition of *Austrobates rivularis,* using either morphological characters alone or with COI sequence data, and found the same basal relationships as Andersen & Weir (1994a). However, when DNA sequence data were analyzed alone, they obtained different results depending on whether they used parsimony (*Austrobates* sister to *Halobates* s.l.) or maximum likelihood (*Austrobates* nested within *Halobates* s.l.). Our molecular evidence indicates a high support for the position of *Austrobates* nested within *Halobates*. We therefore propose the synonymy of these two genera.

Taxonomic status of Ventidius

Our phylogenetic analyses inferred the paraphyly of *Ventidius*. Specifically, *Ventidius* s.str. was more closely related to the *Asclepios* + *Halobates* clade (Halobatini), but *Ventidius* (*Ventidiopsis*) was more closely related to *Esakia*. Historically, Chen & Zettel (1999) down-ranked *Ventidiopsis* to a subgenus of *Ventidius* given that *Ventidiopsis* was a morphological "intermediate" between *Ventidius* (*Ventidius*) and *Ventidius* (*Ventidioides*). However, since *Ventidioides* was not sampled in our study, we decided not to make changes in the current subgeneric status within *Ventidius*.

Ecological evolution in Halobatinae

The subfamily Halobatinae includes the genus *Halobates*, which is almost exclusively marine, living in mangroves, estuaries and lagoons, and with five species adapted to survive on the open ocean often hundreds of kilometers away from land (Andersen & Cheng 2004). Although the open ocean life of some *Halobates* is unparalleled among insects, there are many other gerromorphan bugs living in various coastal marine environments (e.g. Hebridae, Mesoveliidae, Hermatobatidae, Veliidae (subfamilies Haloveliinae, Microveliinae, and Rhagoveliinae), Gerridae (subfamilies Rhagadotarsinae and Trepobatinae; Andersen & J. T. Polhemus 1976; Cheng 1977; Andersen 1982; J. T. Polhemus & D. A. Polhemus 1989; Spence & Andersen 1994; J. T. Polhemus & D. A. Polhemus 2006).

Our results support the hypothesis proposed by Andersen (1991) that marine Halobatini (i.e. *Asclepios* + *Halobates*) evolved from freshwater ancestors and invaded nearshore habitats from lotic (probably estuarine) waters. Metrocorini, however, are only known to live in lotic freshwater habitats in mountains, as well as coastal low-
AQ2 lands. A few species of *Esakia* and *Ventidius* are occasionally found in intertidal regions of river deltas or mangroves (Yang *et al.* 1999; Tran *et al.* 2015; HZ unpublished), indicating a tolerance to salinity that was likely present in the ancestors of *Asclepios* + *Halobates*.

Historical biogeography of Halobatinae

Halobatinae is sister to Ptilomerinae within the Gerridae (Damgaard 2008). The latter is distributed mostly in Asia, with a single genus occurring in Madagascar (*Potamometroides* Hungerford, 1951). Members of Metrocorini are widely distributed in the Afrotropical region and in South and Southeast Asia but absent from the Australian Region, and only *Metrocoris* and *Ventidius* occur beyond the Wallace's line. When the present distribution of freshwater relatives of the sea skaters is taken into account, it seems most likely that the first members of the Halobatini originated in eastern Gondwana, perhaps in the area that now comprises the Indo-Australian region.

While pelagic sea skaters are undoubtedly the most well-known members of the subfamily Halobatinae, the majority of *Halobates* species live in coastal lagoons, estuaries and mangroves (Cheng 1985), and some species often occur in sympatry with *Asclepios* species in coastal areas of southeastern Asia (Andersen & Cheng 2004).

Most coastal *Halobates* species are widely distributed along island arcs in the Indo-Pacific, but some are endemic to islands or island groups (Ikawa *et al.* 2012). The three limnic species are all found in Australia (Andersen & Cheng 2004). Pelagic *Halobates* are among the most fascinating of all insects, living on the ocean surface often at enormous distances from the nearest coast (Herring 1961; Andersen & J. T. Polhemus 1976; Andersen 1982; Cheng 1985, 1989a; Andersen & Cheng 2004). There are five known oceanic species, each with rather well defined distribution ranges (Cheng, 1989b): *H. micans* Eschscholtz, 1822, cosmopolitan and found in all three major

oceans; *H. germanus* White, 1883, confined to the Indian and western Pacific Oceans; *H. sericeus* Eschscholtz, 1822, disjunct distributions in the northern and southern Pacific Ocean; and *H. sobrinus* White, 1883 and *H. splendens* Witlaczil, 1886, both restricted to the eastern tropical Pacific Ocean (see Appendix 1).

The general distribution of *Halobates* covers the entire tropical and subtropical Indo-Pacific Oceans except for *H. micans,* which also occurs in the Atlantic Ocean, including the Caribbean and the Gulf of Mexico (Cheng & Wormuth 1992). This wide range reflects not only the widespread occurrence of the five open-ocean species, but also that of several endemic coastal species (e.g. in the Red Sea and the Galapagos Islands; Ikawa *et al.* 2012). It is therefore difficult to delimit a geographic area of origin for oceanic *Halobates* based on its present distribution.

Halobatinae fossils

The only currently valid fossil Halobatinae is *Halobates ruffoi* Andersen, Farma, Minelli & Piccoli, 1994, discovered in a middle-upper Eocene deposit in northern Italy. Overall, this suggests that sea skaters were present in the Mediterranean region at least 45 mya. This fossil was well preserved, agreed with the extant *Halobates rivularis* in many aspects, and measured 5.8 mm by 2.3 mm, well within those of extant *Halobates* (Cheng *et al.* 2012). *Halobates bagonensis* Lin, 1981, described from Miocene Lunpola Basin in western China, was later found to be an exuviae of the contemporaneous *Aquarius lunpolaensis* Lin, 1981 (Andersen 1998; Cai *et al.* in press).

Conclusion

Because of the unique biology of *Halobates* and its relatives, this genus has been the subject of many phylogenetic studies using morphological (Andersen 1991; Andersen & Weir 1994a), molecular (Andersen *et al.* 2000), or combined analyses (Damgaard *et al.* 2000). Results of these studies have been reviewed in detail by Andersen & Cheng (2004) and are not repeated here, except for a number of new species groups that we have proposed based on the present study (Appendix 2). The phylogenetic trees we present here support the monophyly of Halobatini but Metrocorini in its previously known classification turned out to be paraphyletic. Our results indicate that *Esakia* and *Ventidius* are more closely related to Halobatini *sensu auct*. However, future studies including a better sampling within Metrocorini should be conducted before reaching conclusions on its tribal status. Based on our results, we propose the synonymy of both *Austrobates* and *Halobates* (*Hilliella*) with *Halobates* s.str. These taxonomic changes are intended to reflect the phylogenetic relatedness among the Halobatinae species available for our study. We recommend that future studies on Halobatinae systematics should include (i) species from *Eurymetropsis, Eurymetropsiella*, and *Eurymetropsielloides*, (ii) additional taxa from *Ventidioides* and *Esakia*, in addition to (ii) a larger taxonomic sampling at species level than we were able to obtain, especially for the highly diverse *Metrocoris*.

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Catalogue of World Halobatinae

Appendix 1 to: Román-Palacios *et al.* Molecular phylogeny of sea-skaters (*Halobates* Eschscholtz, 1822), relationship between Halobatini and Metrocorini, and catalogue of the subfamily Halobatinae (Hemiptera: Heteroptera: Gerridae).

compiled until 2004 by Nils Møller Andersen[1]

updated by Felipe Moreira and Herbert Zettel

Abbreviations and symbols used on the catalogue are as follows: holotype (HT), lectotype (LT), neotype (NT), syntypes (ST), male (♂), female (♀), synonymized by (syn.), Afrotropical Region (AF), eastern part of the Palearctic Region (AS), Australasian Region (AU), Nearctic Region (NA), Neotropical Region (NR), Oriental Region (OR), Palearctic Region (PA), archipelago (Arch.), island, islands, or island group (Is.), first record (!), references (Ref.) [references cited directly under the species names are not repeated in the references sections].

AMNH	American Museum of Natural History, New York, New York, U. S. A.
AMS	Australian Museum, Sydney, New South Wales, Australia.
ANIC	Australian National Insect Collection, CSIRO, Canberra, Australia.
BMNH	The Natural History Museum (formerly British Museum, Natural History), London, U. K.
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, U. S. A.
BSAC	Babu Shivnath Agrawal College, Mathura, Uttar Pradesh, India.
CASC	California Academy of Sciences, San Francisco, California, U. S. A.
FMNH	Field Museum, Chicago, Illinois, U. S. A.
HNHM	Hungarian Natural History Museum, Budapest, Hungary.
HUJ	Hebrew University, Jerusalem, Israel.
ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.
IZBE	Estonian University of Life Sciences, Tartu, Estonia.
JTPC	John T. Polhemus Collection (transferred to USNM).
KUEC	Kyushu University, Fukuoka, Japan.
MCVR	Museo Civico di Storia Naturale, Verona, Italy.
MD	Museu Regional do Dundo, Dundo, Luanda Norte, Angola.
MIZT	Museo ed Instituto di Zoologia di Torino, Torino, Italy.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium.
NHMW	Natural History Museum, Vienna, Austria.
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden.
NKUM	Nankai University, Tianjin, China.
NTMD	Northern Territory Museum of Art and Science, Darwin, Australia.
NZSI	National Zoological Collection, Zoological Survey of India, Calcutta, India.

[1] Nils Møller Andersen contributed greatly to our understanding of *Halobates* (Cheng 2008). Sadly, he passed away in 2004. We would like to dedicate this paper to his memory and acknowledge that this catalogue is very much based on his unpublished work.

OUM University Museum of Natural History, Oxford, U. K.
PPCC Ping-ping Chen Collection, Tiel, The Netherlands.
RMNH Nationaal Naturhistorische Museum ("Naturalis"; formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands.
SEMC Snow Entomological Museum, University of Kansas, Lawrence, Kansas, U. S. A.
UPLB Museum of Natural History, University of the Philippines, Los Baños, Laguna, Philippines.
USNM National Museum of Natural History, Smithsonian Institution, Washington D. C., U. S. A.
ZMAN Universiteit van Amsterdam, Zoologisch Museum, Amsterdam, The Netherlands.
ZMHU Zoological Collection, Biological Museum, Hanoi University of Science, Hanoi, Vietnam.
ZMLU Lunds Universitet, Lund, Sweden.
ZMPA Polish Academy of Sciences, Warszawa, Poland.
ZMUC Zoological Museum, University of Copenhagen, Copenhagen, Denmark.
ZMUH Zoologisches Institut und Zoologisches Museum, Universität von Hamburg, Hamburg, Germany.

Infraorder GERROMORPHA Popov, 1971

Family GERRIDAE Leach, 1815

Subfamily Halobatinae Bianchi, 1896 (2 tribes, 9 genera, 3 subgenera, 178 species, 4 subspecies)

Tribe Halobatini Bianchi, 1896 (2 genera, 52 species)

Genus ***Asclepios*** Distant, 1915 (3 species)

Asclepios Distant, 1915: 504. – Type species by monotypy: *Asclepios annandalei* Distant, 1915.

Asclepios annandalei Distant, 1915

Asclepios annandalei Distant, 1915: 505. – LT (Andersen & Foster, 1992: 549): ♂, India, Madras, "Ennar" [Ennur]; BMNH.

DISTRIBUTION: **OR:** India (Andaman Is.! [South Andaman Is.], Tamil Nadu, West Bengal), Malaysia (Kedah, Sabah), Singapore, Sri Lanka (Northern), Thailand (Krabi!, Phuket, Ranong, Satun, Trang).

Ref.: Esaki, 1933; 1937a; Fernando, 1974; Gupta, 1981a; J. T. Polhemus & Cheng, 1982; Andersen, 1991a; Andersen & Foster, 1992; Bal & Basu, 1994; Chen & Zettel, 1998; Thirumalai, 1999; Damgaard *et al.*, 2000; Thirumalai & Krishnan, 2000;

Cheng *et al.*, 2001; Thirumalai, 2002; Chen *et al.*, 2005; Andersen & Cheng, 2004; Damgaard, 2008; Zettel & Tran, 2009; Sites & Vitheepradit, 2010; Ikawa *et al.*, 2012b; Mitra *et al.*, 2016.

Note. The first records from Andaman Islands and Krabi are based on specimens deposited respectively in the ZMUC and the NHMW.

Asclepios apicalis (Esaki, 1924)

Halobates apicalis Esaki, 1924: 112. – HT: ♂, Taiwan (South), Ampin near Tainan; KUEC.
Asclepios apicalis (Esaki, 1924); Esaki, 1930a: 161.
Halobates (*Hilliella*) *apicalis* Esaki, 1924; China, 1957: 343.
Asclepios apicalis (Esaki, 1924); Matsuda, 1960: 297.

DISTRIBUTION. **AS:** Taiwan (Tainan); **OR:** Vietnam (Nam Định!, Quảng Ninh).

Ref.: Esaki, 1926b; 1932; 1933; 1937a; Hoffmann, 1941; Chen & Andersen, 1993; Chen *et al.*, 1993; Aukema & Rieger, 1995; Zettel & Chen, 1996; Hua, 2000; Andersen & Cheng, 2004; Hutacharern *et al.* 2007; Ikawa *et al.*, 2012b.

Note. The record from Nam Định is based on specimens deposited in the NHMW that were kindly donated by Dr. Tran, University of Hanoi.

Asclepios shiranui (Esaki, 1924)

Halobates shiranui Esaki, 1924: 114. – HT: ♀, Japan (Kyushu), Province of Hizen, Masaru near "Saseho" [Sasebo]; KUEC.
Asclepios coreanus Esaki, 1930a: 158 (syn. Hayashi & Miyamoto, 2005: 362). – HT: ♂, Korea, Chungcheongnam-do, "Anminto" [Anmyeondo]; KUEC.
Asclepios shiranui (Esaki, 1924); Esaki, 1930a: 161.
Asclepios coreanus miyamotoi Esaki, 1937a: 135 (syn. Esaki, 1950: 241). – HT: ♂, Japan (Honshu), Province of Suo, Murozumi; KUEC.
Asclepios shiranui shiranui (Esaki, 1924); Esaki, 1950: 241 (syn. Hayashi & Miyamoto, 2005: 362).
Asclepios shiranui coreanus Esaki, 1930; Esaki, 1950: 241 (syn. Hayashi & Miyamoto, 2005: 362).

DISTRIBUTION. **AS:** China (Hong Kong), Japan (Honshu Is., Kyushu Is., Tsushima Is.), South Korea (Chungcheongnam-do, Incheon, Jeollabuk-do).

Ref.: Esaki, 1933; Usinger, 1938; Yamada, 1939; Hoffmann, 1941; Miyamoto, 1957; Miyamoto & Senta, 1960; Matsuda, 1960; Miyamoto, 1961; 1962; Miyamoto & Lee, 1963; Cheng & Hill, 1980; Newman & Cheng, 1983; Andersen, 1991a; Chen & Andersen, 1993; Chen *et al.*, 1993; Lee & Kwon, 1994; Aukema & Rieger, 1995; Kwon *et al.*, 1996; Hayashi & Miyamoto, 1997; Muraji & Tachikawa, 2000; Hua, 2000; Bae & Lee, 2001; Kwon *et al.*, 2001; Nakatani, 2001; Andersen & Cheng,

2004; Damgaard *et al.*, 2005; Bae *et al.*, 2005; BCJ, 2010; Ikawa, 2010; Jung *et al.*, 2011; Ikawa *et al.*, 2012a; 2012b; Lee *et al.*, 2013; Matsuda & Kawano, 2014; Ikawa & Nakazawa, 2015; ECCIJ, 2016; Fairbairn *et al.*, 2016; Morton, 2016.

Genus ***Halobates*** Eschscholtz, 1822 (49 species)

Halobates Eschscholtz, 1822 [1823]: 106. – Type species by subsequent designation (Laporte, 1832: 24): *Halobates micans* Eschscholtz, 1822.
Euratas Distant, 1910a: 146 (syn. Esaki, 1929: 417). – Type species by monotypy: *Euratas formidabilis* Distant, 1910.
Fabatus Distant, 1910a: 147 (syn. Annandale & Kemp, 1915: 183). – Type species by monotypy: *Fabatus servus* Distant, 1910.
Halobates (*Hilliella*) China, 1957: 342 (**new synonym**). – Type species by original designation: *Halobates mjobergi* Hale, 1925.
Austrobates Andersen & Weir, 1994a: 1 (**new synonym**). – Type species by original designation and monotypy: *Austrobates rivularis* Andersen & Weir, 1994.

Halobates acherontis J. T. Polhemus, 1982

Halobates acherontis J. T. Polhemus, 1982: 6. – HT: ♂, Australia, Northern Territory, Daly River; ANIC.

DISTRIBUTION. **AU:** Australia (Northern Territory).

Ref.: Noonan, 1984; Cheng, 1985; Malipatil, 1988; Cheng, 1989; Andersen, 1991b; Andersen & Weir, 1994b; Cassis & Gross, 1995; Andersen & Cheng, 2004; Andersen & Weir, 2004; Cheng, 2006; 2008; J. T. Polhemus & D. A. Polhemus, 2008; Ikawa *et al.*, 2012b; Palacios & Lopez, 2015; Ung *et al.*, 2016.

Halobates alluaudi Bergroth, 1893

Halobates alluaudi Bergroth, 1893: 204. – ST: ♂♀, Seychelles, Praslin; MNHN. AQ3

Halobates princeps; Esaki, 1928a: 74 (misidentification).

DISTRIBUTION. **AF:** Comoros, Europa Is., Kenya, Madagascar, Mozambique, Réunion Is., Seychelles (Aldabra Atoll, Amirante Is., Aride Is., Coëtivy Is., Cosmoledo Atoll, Curieuse Is., D'Arros Is., La Digue Is., Mahé Is., Praslin Is.).

Ref.: Lethierry & Severin, 1896; Kirkaldy, 1899; Herring, 1961; Cheng, 1985; 1989; D. A. Polhemus, 1990b; Cheng, 1991; D. A. Polhemus & J. T. Polhemus, 1991; Andersen, 1991a; 1991b; Andersen & Foster, 1992; Andersen, 1998a; Bowler *et al.*, 1999; Damgaard *et al.*, 2000; Andersen & Cheng, 2004; Ikawa *et al.*, 2008; Ikawa *et al.*, 2012b; D. A. Polhemus & J. T. Polhemus, 2013; Palacios & Lopez, 2015.

Note. This species was erroneously/questionably recorded from Chagos Arch., Sudan, and Papua New Guinea (Distant 1909; 1913; Esaki 1926a).

Halobates browni Herring, 1961

Halobates browni Herring, 1961: 270. – HT: ♂, Solomon Islands, Kolombangara Island, Webster Cove; BMNH.

DISTRIBUTION. **AU:** Solomon Is. (New Georgia Is.).

Ref.: Cheng, 1985; 1989; Andersen & Cheng, 2004; Chen *et al.*, 2005; D. A. Polhemus *et al.*, 2008; Cheng, 2008; Ikawa *et al.*, 2012b.

Halobates bryani Herring, 1961

Halobates bryani Herring, 1961: 286. – HT: ♂, Fiji Islands, Matuku Island; BPBM.

DISTRIBUTION. **AU:** Fiji (Lau Is., Viti Levu Is.).

Ref.: Cheng, 1985; 1989; Andersen, 1991a; 1998a; Damgaard *et al.*, 2000; Andersen & Cheng, 2004; Evenhuis & D. A. Polhemus, 2006; Zettel, 2007; Cheng, 2008; Ikawa *et al.*, 2012b; Palacios & Lopez, 2015.

Halobates calyptus Herring, 1961

Halobates calyptus Herring, 1961: 285. – HT: ♂, Philippines, Mindoro, Varadero Harbor; USNM.

DISTRIBUTION. **OR:** Indonesia (Lesser Sunda Is., Moluccas Arch., Sulawesi Is.), Philippines (Cebu Is., Dinagat Is., Leyte Is., Luzon Is., Mindanao Is., Mindoro Is.); **AU:** Australia (Northern Territory), Indonesia (Papua), Papua New Guinea (Bismarck Arch., D'Entrecasteaux Is., Louisiade Arch., Marshall Bennett Is., Milne Bay, Morobe, Oro, Sandaun, West New Britain), Solomon Is. (Choiseul Is., New Georgia Is.).

Ref.: Cheng, 1985; 1989; J. T. Polhemus & D. A. Polhemus, 1991; Andersen & Cheng, 2004; Andersen & Weir, 2004; Chen *et al.*, 2005; J. T. Polhemus & D. A. Polhemus, 2006; D. A. Polhemus *et al.*, 2008; Ikawa *et al.*, 2012b; Zettel, 2014; Bendanillo *et al.*, 2016.

Halobates darwini Herring, 1961

Halobates darwini Herring, 1961: 278. – HT: ♂, Australia, Northern Territory, Port Darwin; BMNH.

DISTRIBUTION. **AU:** Australia (Northern Territory, Queensland, Western Australia), Papua New Guinea.

Ref.: J. T. Polhemus, 1982; Cheng, 1985; Malipatil, 1988; Cheng, 1989; Andersen, 1991a; 1991b; Andersen & Weir, 1994b; Cassis & Gross, 1995; Andersen, 1998a; Andersen & Cheng, 2004; Andersen & Weir, 2004; Ikawa *et al.*, 2012b; Ung *et al.*, 2016.

Halobates dianae Zettel, 2001

Halobates peronis; Herring, 1961: 278 (in part, paratypes from the Philippines).
Halobates dianae Zettel, 2001: 1097. – HT: ♂, Philippines, Luzon, Camarines Sur, Lagonoy, San Sebastian; UPLB.

DISTRIBUTION. **OR:** Philippines (Bantayan Is., Bohol Is., Camotes Is., Cebu Is., Leyte Is., Luzon Is., Masbate Is., Siquijor Is.).

Ref.: Andersen & Cheng, 2004; Chen *et al.*, 2005; Cheng, 2008; Ikawa *et al.*, 2012b; Zettel, 2014.

Halobates elephanta Andersen & Foster, 1992

Halobates elephanta Andersen & Foster, 1992: 537. – HT: ♂, India, "Bombay" [Mumbai], Elephanta Island; ZMUC.

DISTRIBUTION: AS: Iran (Hormozgan); **OR:** Andaman Sea, India (Maharashtra).

Ref.: Thirumalai, 2002; Andersen & Cheng, 2004; Radhakrishna & Thirumalai, 2004; Linnavuori, 2004; Cheng, 2008; Chandra *et al.*, 2012; Ikawa *et al.*, 2012b; Balakrishnan *et al.*, 2012; Ghahari *et al.*, 2013; Aukema *et al.*, 2013.

Halobates esakii Miyamoto, 1967

Halobates esakii Miyamoto, 1967: 241. – HT: ♂, Brunei, Muara; KUEC.

DISTRIBUTION: **OR:** Brunei (Brunei-Muara), Indonesia (Moluccas Arch.), Malaysia (Kedah), Philippines (Luzon Is., Polillo Is.), Singapore, Thailand (Phuket).

Ref.: Cheng, 1985; 1989; Andersen, 1991a; Andersen & Foster, 1992; Cheng *et al.*, 2001; Andersen & Cheng, 2004; Zettel, 2005; Chen *et al.*, 2005; Cheng, 2008; Zettel & Tran, 2009; Ikawa *et al.*, 2012b; Zettel, 2014.

Halobates fijiensis Herring, 1958

Halobates fijiensis Herring, 1958: 10. – HT: ♂, Fiji Islands, Suva Harbor; ZMUC.

DISTRIBUTION: **AU:** Fiji (Vanua Levu Is., Viti Levu Is.).

Ref.: Herring, 1961; J. T. Polhemus & Cheng, 1982; Holland *et al.*, 1983; Cheng, 1985; Foster & Treherne, 1986; Cheng, 1989; Andersen, 1991a; 1991b; 1998a; Andersen & Cheng, 2004; Evenuis & D. A. Polhemus, 2006; Zettel, 2007; Cheng, 2008; Ikawa *et al.*, 2012b; Ung *et al.*, 2016.

Halobates flaviventris Eschscholtz, 1822

Halobates flaviventris Eschscholtz, 1822: 109. – ST: ♂♀, "South Atlantic" [incorrect locality]; IZBE.

?*Halobates flaviventris* var. *kudrini* Nasonov, 1894: 2 (syn. Herring, 1961: 298). – AQ4 ST: ♀♂, "Pacific Ocean"; repository unknown.

Halobates herdmani Carpenter, 1906: 151 (syn. Esaki, 1928b: 513). – ST: ♀♂, AQ5 "Ceylon" [Sri Lanka]; BMNH.

Halobates eschscholtzi Herring, 1961: 254 (syn. D. A. Polhemus & J. T. Polhemus, 1991: 222). – HT: ♀, Tanzania, Zanzibar, Latham Island; BMNH.

DISTRIBUTION: **OR:** Christmas Is., India (Bay of Bengal, Nicobar Is., Tamil Nadu, West Bengal), Indonesia (Java Is., Moluccas Arch.), Sri Lanka (Eastern, Northern, North Western, Southern, Western), Thailand (Gulf of Thailand, Phuket), Vietnam (Khánh Hòa); **AU:** Marianas (Pagans Is.), New Caledonia (North, South), Palau (Koror), Papua New Guinea (Bismarck Arch.), Vanuatu (Banks Is., Maewo Is.); **AF:** Comoros (Anjouan Is.), Europa Is., Kenya (Coast), Madagascar (Atsimo-Andrefana), Mozambique, Seychelles (Aldabra Atoll, Amirante Is., Cosmoledo Atoll, D'Arros Is., Desroches Is.), Somalia (Banaadir), South Africa, Tanzania (Sange Is., Zanzibar Arch.).

Ref.: Laporte, 1832; Burmeister, 1835; Herrich-Schäffer, 1847; Dohrn, 1859; Frauenfeld, 1867; Walker, 1873; White, 1883; Gerstaecker, 1892; Dahl, 1893; Lethierry & Severin, 1896; Kirkaldy, 1899; Distant, 1903a; Kirkaldy, 1908; Distant, 1910b; Lundbeck, 1914; Distant, 1920; Esaki, 1933; Imms, 1936; Usinger, 1938; Poisson, 1957a; 1959; Matsuda, 1960; Poisson, 1965; Bigot, 1971; Weidner, 1972; Cheng, 1972; 1973b; 1974a; Fernando, 1974; Gross, 1975; Andersen, 1976; 1977; Schulz-Baldes & Cheng, 1981; Cheng, 1981; J. T. Polhemus & Cheng, 1982; Andersen, 1982; Newman & Cheng, 1983; Cheng, 1985; 1989; Cheng *et al.*, 1990; D. A. Polhemus, 1990b; Andersen, 1991a; Andersen & Foster, 1992; Bal & Basu, 1994; Zettel & Chen, 1996; Andersen, 1998a; Chen & Zettel, 1998; Thirumalai, 1999; Damgaard *et al.*, 2000; Thirumalai & Krishnan, 2000; Andersen, 2001; Thirumalai, 2002; Cheng & Mathis, 2003; Andersen & Cheng, 2004; Radhakrishnan & Thirumalai, 2004; Nieser & Chen, 2005; Chen *et al.*, 2005; Hutacharern *et al.* 2007; Cheng, 2008; Evenhuis *et al.*, 2010; Sites & Vitheepradit, 2010; Cheng *et al.*, 2011; Ikawa *et al.*, 2012b; Balakrishnan *et al.*, 2012; D. A. Polhemus & J. T. Polhemus, 2013; Palacios & Lopez, 2015; Fairbairn *et al.*, 2016; Mitra *et al.*, 2016.

Note. Records from the Atlantic Ocean are incorrect.

Halobates formidabilis (Distant, 1910)

Euratas formidabilis Distant, 1910a: 147. – LT (Andersen & Foster, 1992: 542): ♂, Andaman Sea; BMNH.

Fabatus servus Distant, 1910a: 147 (syn. Annandale & Kemp, 1915: 183). – ST [nymphs]: Andaman Sea; BMNH.

Halobates formidabilis (Distant, 1910); Esaki, 1929: 416.

Halobates galatea Herring, 1961: 294 (in part, allotype ♀, "Bombay" [Mumbai]).

DISTRIBUTION: **OR:** Andaman Sea, India (Andaman Is. [Ross Is.], Bay of Bengal, Andhra Pradesh, Maharashtra, Odisha), Maldives (Addu Atoll, Alif Alif Atoll), Sri Lanka (Northern).

Ref.: Distant, 1910b; Annandale, 1911; Esaki, 1933; Usinger, 1938; Fernando, 1974; J. T. Polhemus & Cheng, 1982; 1985; 1989; Andersen, 1991a; Thirumalai & Krishnan, 2000; Thirumalai, 2002; Andersen & Cheng, 2004; Radhakrishnan & Thirumalai, 2004; Cheng, 2008; Chandra *et al.*, 2012; Ikawa *et al.*, 2012b; Balakrishnan *et al.*, 2012; Rao *et al.*, 2013.

Note. This species was recorded from French Polynesia (Tuamotu Arch.) by Cheng (1989), but the record was unconsidered by Andersen & Cheng (2004) and Ikawa *et al.* (2012b), a decision that is followed here.

Halobates galatea Herring, 1961

Halobates galatea Herring, 1961: 294. – HT: ♂, Arabian Sea; BMNH.

DISTRIBUTION: **OR:** Arabian Sea, India (Goa, Kerala, Maharashtra), Sri Lanka.

Ref.: Cheng, 1985; 1989; Andersen, 1991a; Andersen & Foster, 1992; Thirumalai & Krishnan, 2000; Thirumalai, 2002; Andersen & Cheng, 2004; Radhakrishnan & Thirumalai, 2004; Cheng, 2008; Ikawa *et al.*, 2012b; Balakrishnan *et al.*, 2012.

Halobates germanus White, 1883

Halobates germanus White, 1883: 50. – HT: ♀, North Pacific Ocean; BMNH.
?*Halobates germanus* var. *bankae* Griffini, 1895: 3 (syn. Herring, 1961: 240). – ST: ♀♂, Indonesia, "Stretto di Banka" [Bangka Strait]; MIZT. AQ6
Halobates sewelli Imms, 1936: 71 (syn. Herring, 1961: 253). – HT: ♂, Gulf of Oman, Arabian Sea; BMNH.
Halobates sericeus; Poisson, 1965: 1497 (misidentification).

DISTRIBUTION. **AS:** Arabian Sea, China (East and South China Sea), Gulf of Aqaba (Egypt, Israel, Saudi Arabia), Iran, Japan (Bonin Is., Goto Is., Honshu Is., Kyushu Is., Ryukyu Arch., Shikoku Is.), Oman (Gulf of Oman), Red Sea (Egypt, Saudi Arabia, Sudan, Yemen); **OR:** Andaman Sea, Bali Sea, Banda Sea, Bay of Bengal, Celebes Sea, India (Gujarat, Maharashtra, Tamil Nadu), Indonesia (Bangka Strait, Borneo Is., Java Is., Lesser Sunda Is., Malacca Strait, Moluccas Arch., Natuna Is., Sulawesi Is., Sumatra Is.), Java Sea, Malaysia (Peninsular Malaysia, Sarawak), Maldives, Philippines (Luzon Is., Mindanao Is., Palawan Is.), Singapore, Sri Lanka, Sulu Sea, Thailand (Gulf of Thailand), Vietnam; **AU:** Australia (Northern Territory, Queensland, Western Australia), Cook Is., French Polynesia (Gambier Is., Society Is., Tuamotu Arch.), Fiji, Indonesia (Papua), New Caledonia (North, South), Palau, Papua New Guinea (Bismarck Arch., Louisiade Arch.), Samoa, Solomon Is., Tonga, Vanuatu (Maewo Is.), West and Central Pacific Ocean; **AF:** Indian Ocean, Kenya, Madagascar (Diana), Mauritius, Mozambique, Réunion Is., Seychelles (Aldabra Atoll, Cosmoledo Atoll), Somalia.

Ref.: Dahl, 1893; Lethierry & Severin, 1896; Distant, 1910a; 1910b; 1920; Esaki, 1924; 1933; Hoffmann, 1933; Wu, 1935; Macan, 1937; Usinger, 1938; Hoffmann, 1941; Brown, 1951; Herring, 1958; Matsuda, 1960; Miyamoto & Senta, 1960; Miyamoto, 1961a; 1962; Herring, 1964; Cheng & Fernando, 1969; Cheng, 1971;

Jaczewski, 1972; Schmidt & Müller, 1973; Fernando & Cheng, 1974; Cheng, 1974a; Fernando, 1974; Lee & Cheng, 1974; Nadkarni, 1975; Cheng, 1975; Andersen & J. T. Polhemus, 1976; Tomokuni & Sato, 1978; Cheng & Hill, 1980; Cheng, 1981; Andersen, 1982; Cheng & Holdway, 1983; Newman & Cheng, 1983; Cheng, 1985; Linnavuori, 1986; Malipatil, 1988; Cheng, 1989; Cheng *et al.* 1990; D. A. Polhemus, 1990b; D. A. Polhemus & J. T. Polhemus, 1991; Andersen, 1991a; Andersen & Foster, 1992; Chen & Nieser, 1992; Chen & Andersen, 1993; Chen *et al.*, 1993; Senta *et al.*, 1993; Abu-Zoherah *et al.*, 1993; Andersen & Weir, 1994b; Cheng & Holdway, 1995; Aukema & Rieger, 1995; Cassis & Gross, 1995; Andersen, 1998a; Chen & Zettel, 1998; Chen, 1999; Damgaard *et al.*, 2000; Andersen *et al.*, 2000; Hua, 2000; Cheng *et al.*, 2001; Nakatani, 2001; Andersen, 2001; Thirumalai, 2002; Ikawa *et al.*, 2002; Cheng & Mathis, 2003; Tran & Yang, 2004; Andersen & Cheng, 2004; Andersen & Weir, 2004; Ikawa *et al.*, 2004; Radhakrishnan & Thirumalai, 2004; Chen *et al.*, 2005; Ahmed & Gadalla, 2005; Harada, 2005; J. T. Polhemus & D. A. Polhemus, 2006; Cheng, 2006; Hutacharern *et al.* 2007; Ikawa *et al.*, 2007; 2008; Cheng, 2008; Perez-Goodwyn, 2009; Harada *et al.*, 2011a; 2011b; Nakajima *et al.*, 2011; Cheng *et al.*, 2011; Chandra *et al.*, 2012; Cheng *et al.*, 2012; Ikawa *et al.*, 2012b; Balakrishnan *et al.*, 2012; D. A. Polhemus & J. T. Polhemus, 2013; Ghahari *et al.*, 2013; Nakajo *et al.*, 2013; Harada *et al.*, 2013; Ôhara *et al.*, 2013; Aukema *et al.*, 2013; Damgaard & Zettel, 2014; Zettel, 2014; Balakrishnan *et al.*, 2014; Palacios & Lopez, 2015; Umamoto *et al.*, 2015; Furuki *et al.*, 2016; Harada *et al.*, 2016; Fairbairn *et al.*, 2016; ECCIJ 2016; Furuki *et al.*, 2017; Harada *et al.*, 2017.

Halobates hawaiiensis Usinger, 1938

Halobates hawaiiensis Usinger, 1938: 79. – HT: ♂, Hawaiian Islands, Oahu, Waikiki; BPBM.

DISTRIBUTION. **AU:** French Polynesia (Marquesas Is., Society Is., Tuamotu Arch.), Kiribati (Christmas Is.), Hawaiian Is (Hawaii Is., Kauai Is., Oahu Is.).

Ref.: Williams, 1944; Zimmermann, 1948; Usinger & Herring, 1957; Herring, 1958; Matsuda, 1960; Herring 1961; Andersen & J. T. Polhemus, 1976; J. T. Polhemus & Cheng, 1982; Springer, 1982; Cheng, 1985; 1989; Andersen, 1998a; Damgaard *et al.*, 2000; Andersen, 2001; Englund *et al.*, 2000a; 2000b; Tsoukatou *et al.*, 2001; Petrakis *et al.*, 2003; Andersen & Cheng, 2004; Riley, 2006; Cheng, 2006; 2008; Cheng *et al.*, 2011; Ikawa *et al.*, 2012b; Palacios & Lopez, 2015.

Halobates hayanus White, 1883

Halobates hayanus White, 1883: 52. – HT: ♂, Red Sea, near Aden; BMNH.

AQ7 *Halobates frauenfeldanus* White, 1883: 57 (syn. Herring, 1961: 284). – ST: ♂♀, Indian Ocean near the Nicobar Islands; NHMW.

Halobates incanus Witlaczil, 1886: 172 (syn. Dahl, 1893: 7). – ST: ♂, ♀: Arabian Sea, northeastern and southeastern from Socotra; NHMW?.

Halobates australiensis Malipatil, 1988: 157 (syn. Andersen, 1991a: 45). – HT: ♂, Australia, Northern Territory, Wessel Islands; NTMD.

DISTRIBUTION. **AS:** China (South China Sea), Egypt (Red Sea, South Sinai), Saudi Arabia (Makkah), Yemen (Socotra Is.); **OR:** India (Nicobar Is.), Indonesia (Anamba Is., Bali Is., Borneo Is., Java Is., Lesser Sunda Is., Moluccas Arch., Sulawesi Is.), Malaysia (Johor, Kedah), Philippines (Cebu Is., Luzon Is., Mindanao Is., Palawan Is.), Singapore, Thailand (Krabi, Phuket), Vietnam (Khánh Hòa); **AU:** Australia (Northern Territory, Queensland, Western Australia), East Timor (Dili, Lautem), Indonesia (Papua), Papua New Guinea (D'Entrecasteaux Is., Engineer Group, Louisiade Arch., Milne Bay, Morobe, National Capital District, Sandaun); **AF:** Djibouti, Eritrea (Northern Red Sea), Sudan (Red Sea).

Ref.: Lethierry & Severin, 1896; Distant, 1903a; Esaki, 1926a; 1933; Imms, 1936; Usinger, 1938; Brown, 1951; Matsuda, 1960; Poisson, 1965; Cheng & Fernando, 1969; Linnavuori, 1971; 1973; Schmidt & Müller, 1973; Fernando & Cheng, 1974; Dethier, 1981; Nichols & Johns, 1983; Cheng, 1985; Linnavuori, 1986; Cheng, 1989; Zrzavý, 1990; Andersen & Foster, 1992; Zrzavý, 1992a; 1992b; Abu-Zoherah *et al.*, 1993; Andersen & Weir, 1994b; Aukema & Rieger, 1995; Cassis & Gross, 1995; Zettel & Chen, 1996; Andersen, 1998a; Damgaard *et al.*, 2000; Cheng *et al.*, 2001; Andersen, 2001; Thirumalai, 2002; Tran & Yang, 2004; Andersen & Cheng, 2004; Andersen & Weir, 2004; Radhakrishnan & Thirumalai, 2004; Chen *et al.*, 2005; Ahmed & Gadalla, 2005; J. T. Polhemus & D. A. Polhemus, 2006; Cheng, 2008; Zettel & Tran, 2009; Sites & Vitheepradit, 2010; Chandra *et al.*, 2012; Cheng *et al.*, 2012; Ikawa *et al.*, 2012b; Balakrishnan *et al.*, 2012; Aukema *et al.*, 2013; Brożek & Zettel, 2014; Zettel, 2014; Palacios & Lopez, 2015; Bendanillo *et al.*, 2016.

Note. The record from Ceram (Herring, 1961) concerns *H. calyptus*.

Halobates herringi J. T. Polhemus & Cheng, 1982

Halobates herringi J. T. Polhemus & Cheng, 1982: 224. – HT: ♂, Australia, Queensland, Gladstone, Auckland Creek; ANIC.

DISTRIBUTION. **AU:** Australia (Northern Territory, Queensland), Indonesia (Papua).

Ref.: Cheng, 1985; Malipatil, 1988; Cheng, 1989; Andersen, 1991b; Andersen & Weir, 1994b; Cassis & Gross, 1995; Andersen, 1998a; Andersen & Cheng, 2004; Andersen & Weir, 2004; Cheng, 2008; Ikawa *et al.*, 2012b; Ung *et al.*, 2016.

Halobates japonicus Esaki, 1924

Halobates japonicus Esaki, 1924: 115. – HT: ♂, Japan (Shikoku), Sagami Province, Aburatsubo creek near Misaki; KUEC.

DISTRIBUTION. **AS:** Japan (Honshu Is., Kyushu Is., Ryukyu Arch., Shikoku Is.).

Ref.: Esaki, 1926a; 1932; 1933; Usinger, 1938; Esaki, 1950; 1955; Takara, 1957; Miyamoto & Senta, 1960; Matsuda, 1960; Herring, 1961; Miyamoto, 1961a; 1962; Takara & Azuma, 1972; Cheng, 1985; 1989; Andersen, 1991a; Aukema & Rieger, 1995; Azuma *et al.*, 1996; Nakatani, 2001; Andersen & Cheng, 2004; Hayashi &

Ozaki, 2004; Ikawa *et al.*, 2006; Cheng, 2008; BCJ, 2010; Ikawa *et al.*, 2008; 2012b; Taki *et al.*, 2015; ECCIJ, 2016.

Halobates katherinae Herring, 1958

Halobates katherinae Herring, 1958: 8. – HT: ♂, New Caledonia, Nouville; SEMC.

DISTRIBUTION. **AU:** New Caledonia (Loyalty Is., South), Vanuatu.

Ref.: Herring, 1961; J. T. Polhemus & Cheng, 1982; Cheng, 1985; 1989; Andersen, 1991b; Andersen & Cheng, 2004; Nieser & Chen, 2005; Cheng, 2008; Ikawa *et al.*, 2012b; Damgaard & Zettel, 2014; Ung *et al.*, 2016.

Halobates kelleni Herring, 1961

Halobates princeps; Esaki, 1928a: 74 (misidentification).
Halobates kelleni Herring, 1961: 266. – HT: ♂, Samoa, Tutuila Island; BPBM.

DISTRIBUTION. **AU:** American Samoa (Tutuila Is.), Samoa (Upolu Is.), Tokelau Atolls (Nukunonu Atoll).

Ref.: Hinckley, 1969; J. T. Polhemus & Cheng, 1982; Cheng, 1985; 1989; Andersen 1991b; 1998a; Andersen & Cheng, 2004; Cheng, 2008; Ikawa *et al.*, 2012b; Palacios & Lopez, 2015; Ung *et al.*, 2016.

Halobates lannae Andersen & Weir, 1994

Halobates lannae Andersen & Weir, 1994b: 874. – HT: ♂, Australia, Northern Territory, Darwin, Frances Bay; ANIC.

DISTRIBUTION. **AU:** Australia (Northern Territory, Western Australia), Papua New Guinea.

Ref.: Cassis & Gross, 1995; Andersen, 1998a; Andersen & Weir, 2003; Andersen & Cheng, 2004; Andersen & Weir, 2004; Cheng, 2008; Ikawa *et al.*, 2012b.

Halobates liaoi Zettel, 2005

Halobates liaoi Zettel, 2005: 410. – HT: ♂, Philippines, Surigao del Norte, Dinagat Is., 6.8 km north of Dinagat, Busay; UPLB.

DISTRIBUTION. **OR:** Philippines (Dinagat Is., Hikdop Is.).

Halobates maculatus Schadow, 1922

AQ8 *Halobates maculatus* Schadow, 1922: 2. – ST: ♀♂, Papua New Guinea, Bismarck Arch., St. Matthias, Ekaliu; ZMUH (types lost according to Weidner, 1972).
Halobates rotundatus Esaki, 1926a: 131 (syn. Herring, 1961: 281). – HT, ♂: Papua New Guinea, Dregerhafen; HNHM.

DISTRIBUTION. **OR:** Indonesia (Lesser Sunda Is., Sulawesi Is.), Philippines (Luzon Is., Mindoro Is., Ticao Is.); **AU:** East Timor (Dili), Papua New Guinea (Bismarck Arch., D'Entrecasteaux Is., Conflict Group, Engineer Group, Louisiade Arch., Madang, Milne Bay, Morobe, West New Britain), Solomon Is. (Florida Is., New Georgia Is., Rennell Is.).

Ref.: Usinger, 1938; Cheng & Holdway, 1983; Cheng, 1985; 1989; Andersen, 1991a; Andersen & Cheng, 2004; Zettel, 2005; Chen *et al.*, 2005; J. T. Polhemus & D. A. Polhemus, 2006; D. A. Polhemus *et al.*, 2008; Cheng, 2008; Ikawa *et al.*, 2012b; Zettel, 2014.

Halobates mariannarum Esaki, 1937

Halobates mariannarum Esaki, 1937b: 357. – HT: ♂, Mariana Islands, Rota; KUEC.

DISTRIBUTION. **AU:** Marianas (Guam Is., Rota Is.), Marshall Is. (Arno Atoll), Micronesia (Kosrae Is., Pohnpei Is., Truk Is., Yap Is.), Palau.

Ref.: Usinger, 1938; 1946; 1951; Usinger & La Rivers, 1953; Matsuda, 1960; Herring, 1961; Andersen & J. T. Polhemus, 1976; Cheng, 1981; J. T. Polhemus & Cheng, 1982; Cheng, 1985; 1989; Andersen, 1991a; 1991b; 1998a; Damgaard *et al.*, 2000; Cheng & Mathis, 2003; Andersen & Cheng, 2004; Cheng, 2008; Ikawa, 2009; Ikawa *et al.*, 2012b; Palacios & Lopez, 2015.

Halobates matsumurai Esaki, 1924

Halobates sericeus; Matsumura, 1913: 97; 1930: 76 (misidentifications).
Halobates matsumurai Esaki, 1924: 117. – HT: ♂, "Northern Formosa" [Taiwan (North)], Tansui, near Taihoku; KUEC.
Halobates princeps; Esaki, 1930a: 158; 1932: 1642; 1933: 778; 1950: 241; Yamada, 1939: 61 (misidentifications).

DISTRIBUTION. **AS:** China (East China Sea, South China Sea, Zhoushan Is.), Japan (Honshu Is., Kujukushima Is., Kyushu Is., Tsushima Is.), South Korea (Chungcheongnam-do, Incheon), Taiwan (New Taipei).

Ref.: Esaki, 1926b; Miyamoto & Senta, 1960; Herring, 1961; Miyamoto, 1961a; 1962; Miyamoto & Lee, 1963; Cheng, 1985; 1989; Andersen, 1991a; Chen & Andersen, 1993; Chen *et al.*, 1993; Lee & Kwon, 1994; Aukema & Rieger, 1995; Kwon *et al.*, 1996; Hua, 2000; Muraji & Tachikawa, 2000; Kwon *et al.*, 2001; Nakatani, 2001; Andersen & Cheng, 2004; Cheng, 2008; Ikawa, 2010; BCJ, 2010; Jung *et al.*, 2011; Ikawa *et al.,* 2012a; 2012b; Lee *et al.*, 2013; Palacios & Lopez, 2015; Ikawa & Nakazawa, 2015; ECCIJ, 2016; Cherng, 2016.

Halobates melleus Linnavuori, 1971

Halobates melleus Linnavuori, 1971: 360. – HT: ♂, Egypt, Mersa Hala'ib [area claimed by Sudan]; AMNH.

Halobates mangrovensis Schmidt & Müller, 1973: 6 (syn. Linnavuori, 1980: 2). – HT: ♂, Egypt, El Gharqana mangrove lagoon north of Nabq; HUJ.
Halobates mangrovearum; Linnavuori, 1980: 2 (incorrect subsequent spelling).

DISTRIBUTION. **AS:** Egypt (Red Sea, South Sinai), Gulf of Aqaba, Israel (Southern); Red Sea (Yemen); **AF:** Eritrea (Northern Red Sea).

Ref.: J. T. Polhemus, 1982; Cheng, 1985; 1989; J. T. & D. A. Polhemus, 1991; Andersen & Foster, 1992; Aukema & Rieger, 1995; Andersen & Cheng, 2004; Ahmed & Gadalla, 2005; Cheng, 2008; Cheng *et al.*, 2012; Ikawa *et al.* 2012b; Ghahari *et al.*, 2013; Aukema *et al.*, 2013; Palacios & Lopez, 2015.

Note. This species was listed from Iran by Aukema & Rieger (1995) and Ghahari *et al.* (2013), but the record was unconsidered by Andersen & Cheng (2004) and Ikawa *et al.* (2012b), a decision that is followed here.

Halobates micans Eschscholtz, 1822

AQ9 *Halobates micans* Eschscholtz, 1822: 107. – ST: ♀♂, southern Pacific Ocean and southern Atlantic Ocean; IZBE.

AQ10 *Halobates streatfieldana* Templeton, 1836: 230 (syn. Herring, 1961: 246). – ST: ♀♂, Atlantic Ocean; repository unknown.
Halobates wullerstorffi Frauenfeld, 1867: 458 (syn. Dahl, 1893: 6). – ST: ♂, ♀, Brazil, off Cape Frio near Rio de Janeiro; NHMW.

AQ11 *Halobates inermis* Dahl, 1893: 6 (syn. Schadow, 1922: 1). – HT: ♀♂, Atlantic Ocean; repository unknown.

DISTRIBUTION. Atlantic Ocean, including Caribbean Sea, between 40° N and 40° S, with few records out of these latitudes; Indian Ocean between 20° N and 30–40° S; western Pacific Ocean between 30° N and 20–25° S; central and eastern Pacific Ocean between 35° N and 20° S, with few records out of these latitudes. **AS:** China, Egypt, Japan, Taiwan; **OR:** India, Indonesia, Maldives, Myanmar, Philippines, Sri Lanka, Vietnam; **AU:** American Samoa, Australia, Cook Is., French Polynesia, Indonesia, Kiribati, Marquesas Is., Marshall Is., Micronesia, Palau, Papua New Guinea, Solomon Is.; **AF:** Azores Arch., Cameroon, Canary Is., Cape Verde Is., Juan de Nova Is., Madagascar, Madeira Arch., Mauritania, Mauritius, Saint Helena Is., Seychelles (Aldabra Atoll, Cosmoledo Atoll), Somalia; **NA:** United States of America; **NR:** Antigua & Barbuda, Argentina, Aruba, Bahamas, Barbados, Bermuda, Brazil, Cayman Is., Chile, Clipperton Is., Colombia, Cuba, Ecuador (including Galapagos Is.), French Guiana, Guadeloupe, Martinique, Mexico, Panama, St. Vincent & Grenadines, Trinidad & Tobago, Uruguay, U.S. Virgin Is.; **PA:** Spain.

Ref.: Laporte, 1832; Burmeister, 1835; Blanchard, 1840; Herrich-Schäffer, 1847; Guérin-Méneville, 1857; Dohrn, 1859; Giglioli, 1870; Walker, 1873; Butler, 1881; White, 1883; Uhler, 1884; Girard, 1885; Witlaczil, 1886; Uhler, 1886; Howard, 1889; Walker, 1893a; 1893b; Lethierry & Severin, 1896; Wickham, 1894; Uhler,

1894; Griffini, 1895; Slosson, 1901; Heidemann, 1901; Walker, 1902; Distant, 1903a; Kirkaldy, 1906; Kirkaldy & Torre-Bueno, 1909; Banks, 1910; Torre-Bueno, 1911; Swezey, 1913; Barber, 1914; Lundbeck, 1914; Davis, 1915; Van Duzee, 1916; 1917; Hungerford, 1919; Bryan, 1922; Britton, 1923; Blatchley, 1926; Esaki, 1926a; 1926b; 1933; Barber, 1934; Brimley, 1938; Usinger, 1938; Hoffmann, 1941; Barber, 1943; Van Zwaluwenburg, 1943; Usinger, 1944; Hynes, 1948; Usinger, 1951; Usinger & La Rivers, 1953; Herring, 1958; Miyamoto & Senta, 1960; Matsuda, 1960; Miyamoto, 1961a; Herring, 1964; Poisson, 1965; Linsley & Usinger, 1966; Alayo, 1967; Ashmole & Ashmole, 1967; de Kort-Gommers & Nieser, 1969; Cheng, 1971; Weidner, 1972; Jaczewski, 1972; Cheng, 1972; 1973a; 1973b; 1974a; 1974b; Alayo, 1974; Fernando, 1974; Cheng, 1975; Andersen & J. T. Polhemus, 1976; Andersen, 1977; Cheng & Schulenberger, 1980; Cheng & Maxfield, 1980; Schulz-Baldes & Cheng, 1980; Cheng & Hill, 1980; Linnavuori, 1981; Froeschner, 1981; Dethier, 1981; J. T. Polhemus & Cheng, 1982; Andersen, 1982; Cheng & Holdway, 1983; Newman & Cheng, 1983; Stoner & Humphrys, 1985; Froeschner, 1985; Cheng, 1985; Cheng *et al.*, 1986; Malipatil, 1988; Henry & Froeschner, 1988; Cheng, 1989; Schulz-Baldes, 1989; D. A. Polhemus, 1990b; Cheng *et al.*, 1990; Baena & Baéz, 1990; Henry & Hilburn, 1990; D. A. Polhemus & J. T. Polhemus, 1991; Andersen, 1991a; 1991b; Nieser & Alkins-Koo, 1991; Cheng & Wormuth, 1992; Schulz-Baldes, 1992; Andersen & Foster, 1992; Chen & Andersen, 1993; Chen *et al.*, 1993; Senta *et al.*, 1993; Andersen & Weir, 1994b; Nieser *et al.*, 1994; Aukema & Rieger, 1995; Cheng & Holdway, 1995; Cassis & Gross, 1995; Cheng, 1997; Andersen, 1998a; Ikawa *et al.*, 1998; Froeschner, 1999; Chen, 1999; Hua, 2000; Damgaard *et al.*, 2000; Andersen *et al.*, 2000; Cheng *et al.*, 2001; Peck, 2001; Nakatani, 2001; Andersen, 2001; Thirumalai, 2002; Aristizábal, 2002; Ikawa *et al.*, 2002; Bass, 2003; Cheng & Mathis, 2003; Petrakis *et al.*, 2003; Andersen & Cheng, 2004; Andersen & Weir, 2004; Ikawa *et al.*, 2004; Radhakrishnan & Thirumalai, 2004; Molano-Rendón *et al.*, 2005; Chen *et al.*, 2005; Ahmed & Gadalla, 2005; Harada, 2005; Borges *et al.*, 2005; Arechalaveta *et al.*, 2005; Epler, 2006; Cheng, 2006; Handler *et al.*, 2007; Murata *et al.*, 2007; Ikawa *et al.*, 2007; 2008; Posso & González, 2008; D. A. Polhemus *et al.*, 2008; Molano-Rendón *et al.*, 2008; Damgaard, 2008; Cheng, 2008; Dias & Lopes, 2009; Garrouste & Cheng, 2009; Frick *et al.*, 2009; Naranjo *et al.*, 2010; Cheng *et al.*, 2010; Muñoz *et al.*, 2010; Ruderhousen *et al.*, 2010; Borges *et al.*, 2010; Buzzetti & Cianferoni, 2011; Moreira *et al.*, 2011; Harada *et al.*, 2011a; 2011b; Cheng *et al.*, 2011; Nakajima *et al.*, 2011; Majer *et al.*, 2012; Chandra *et al.*, 2012; Cheng *et al.*, 2012; Balakrishnan *et al.*, 2012; Yamada & Hama, 2012; Naranjo & Serrano, 2012; D. A. Polhemus & J. T. Polhemus, 2013; Ôhara *et al.*, 2013; Nakajo *et al.*, 2013; Sekimoto *et al.*, 2013; Harada *et al.*, 2013; Aukema *et al.*, 2013; Matsuda & Kawano, 2014; Engels *et al.*, 2014; Zettel, 2014; Sekimoto *et al.*, 2014; Takenaka *et al.*, 2014; Balakrishnan *et al.*, 2014; Padilla-Gil, 2015; Palacios & Lopez, 2015; Umamoto *et al.*, 2015; Kiessling *et al.*, 2015; Fairbairn *et al.*, 2016; Furuki *et al.*, 2016; ECCIJ, 2016; Harada *et al.*, 2016; 2017; Furuki *et al.*, 2017; Coscarón, 2017; Vallaeys *et al.*, 2017.

Halobates mjobergi Hale, 1925

Halobates mjobergi Hale, 1925: 12. – HT: ♂, Australia, Western Australia, Broome; NHRS.

DISTRIBUTION. **AU:** Australia (Northern Territory, Queensland, Western Australia), Papua New Guinea.

Ref.: Esaki, 1933; Usinger, 1938; China, 1957; Herring, 1961; J. T. Polhemus, 1982; Cheng, 1985; Malipatil, 1988; Cheng, 1989; Andersen, 1991a; Andersen & Weir, 1994b; Cassis & Gross, 1995; Andersen, 1998a; Damgaard *et al.*, 2000; Andersen & Weir, 2003; 2004; Andersen & Cheng, 2004; Damgaard *et al.*, 2005; Damgaard, 2008; Cheng, 2008; Ikawa *et al.*, 2012b; Palacios & Lopez, 2015.

Halobates murphyi J. T. Polhemus & D. A. Polhemus, 1991

Halobates murphyi J. T. Polhemus & D. A. Polhemus, 1991: 8. – HT: ♂, Papua New Guinea, Morobe Province, Labu Lakes, Markham River estuary; USNM.

DISTRIBUTION. **AU:** Indonesia (Papua), Papua New Guinea (Bismarck Arch., East Sepik, Louisiade Arch., Marshall Bennett Is., Milne Bay, Morobe, Oro, West New Britain).

Ref.: Andersen & Cheng, 2004; J. T. Polhemus & D. A. Polhemus, 2006; 2008; Cheng, 2008; Ikawa *et al.*, 2012b.

Halobates nereis Herring, 1961

Halobates princeps; Esaki, 1937b: 356 (misidentification).
Halobates nereis Herring, 1961: 272. – HT: ♂, Palau, Koror; BPBM.

DISTRIBUTION: **AU:** Palau (Babelthuap, Koror), Papua New Guinea (Madang).

Ref.: Cheng, 1981; Schulz-Baldes & Cheng, 1981; J. T. Polhemus & Cheng, 1982; Cheng, 1985; 1989; Damgaard *et al.*, 2000; Cheng & Mathis, 2003; Andersen & Cheng, 2004; Chen *et al.*, 2005; Cheng, 2008; Ikawa *et al.*, 2012b; Palacios & Lopez, 2015.

Halobates panope Herring, 1961

Halobates panope Herring, 1961: 295. – HT: ♂, New Caledonia, stream estuary between Touho and Ponerihouen; SEMC.

DISTRIBUTION. **AU:** New Caledonia (North, South).

Ref.: J. T. Polhemus & Cheng, 1982; Cheng, 1985; 1989; Andersen, 1991a; Andersen & Cheng, 2004; Cheng, 2008; Ikawa *et al.*, 2012b; Damgaard & Zettel, 2014.

Halobates peronis Herring, 1961

Halobates peronis Herring, 1961: 278. – HT: ♂, Solomon Islands, San Cristobal Island, Star Harbor; BMNH.

DISTRIBUTION. **AU:** Papua New Guinea (Bismarck Arch.), Solomon Islands (Florida Is., New Georgia Is., San Cristobal Is., Santa Isabel Is.).

Ref.: Cheng, 1985; 1989; Andersen, 1991a; 1991b; 1998a; Andersen & Cheng, 2004; Chen *et al.*, 2005; D. A. Polhemus *et al.*, 2008; Cheng, 2008; Ikawa *et al.*, 2012b; Ung *et al.*, 2016.

Note. Paratypes from the Philippines determined by Herring (1961) have later been described as *H. dianae*.

Halobates poseidon Herring, 1961

Halobates poseidon Herring, 1961: 287. – HT: ♂, Kenya, Mombasa Island, Port Tudor; BMNH.

DISTRIBUTION. **AF:** Kenya (Kilifi, Mombasa), Madagascar, Mozambique, Seychelles (Aldabra Atoll, Cosmoledo Atoll, granitic islands), Tanzania (Tanga).

Ref.: Linnavuori, 1971; J. T. Polhemus & Cheng, 1982; Cheng, 1985; 1989; D. A. Polhemus, 1990b; D. A. Polhemus & J. T. Polhemus, 1991; Andersen, 1991a; Andersen & Foster, 1992; Damgaard *et al.*, 2000; Andersen & Cheng, 2004; Cheng, 2008; Ikawa *et al.*, 2012b; D. A. Polhemus & J. T. Polhemus, 2013; Palacios & Lopez, 2015.

Halobates princeps White, 1883

Halobates princeps White, 1883: 44, 80. – HT: ♀, Indonesia, "Celebes Sea" [Sulawesi]; BMNH.
Halobates ashmorensis Malipatil, 1988: 158 (syn. Andersen, 1991a: 45). – HT: ♂, Australia, Northern Territory, Ashmore Reef; NTMD.

DISTRIBUTION. **OR:** Banda Sea, Christmas Is., India (Nicobar Is., Odisha), Indonesia (Borneo Is., Celebes Sea, Java Is., Lesser Sunda Is., Madura Is., Moluccas Arch., Sangihe Is., Sulawesi Is., Sumatra Is.), Malaysia (Sabah), Philippines (Burias Is., Panglao Is.), Singapore, Sri Lanka, Thailand; **AU:** Australia (Northern Territory, Queensland, Western Australia), East Timor (Dili, Lautem), Indonesia (Papua, West Papua), Palau, Papua New Guinea (Bismarck Arch., Conflict Group, D'Entrecasteaux Is., Engineer Group, Louisiade Arch., Milne Bay, West New Britain), Solomon Is. (Choiseul Is., Malaita Is., New Georgia Is.), Vanuatu.

Ref.: Dahl, 1893; Walker, 1893a; Lethierry & Severin, 1896; Kirby, 1900; Kirkaldy, 1901a; Izzard, 1936; Mathur, 1953; Herring, 1961; Cobben, 1978; Cheng, 1981;

Cheng & Schmitt, 1982; Cheng & Holdway, 1983; Cheng, 1985; 1989; Cheng *et al.*, 1990; J. T. Polhemus & D. A. Polhemus, 1991; Andersen, 1991b; Andersen & Foster, 1992; Chen & Nieser, 1992; Andersen & Weir, 1994b; Cassis & Gross, 1995; Andersen, 1998a; Cheng *et al.* 2001; Turner *et al.*, 2001; Cheng & Mathis, 2003; Andersen & Cheng, 2004; Andersen & Weir, 2004; Chen *et al.*, 2005; Zettel, 2005; J. T. Polhemus & D. A. Polhemus, 2006; D. A. Polhemus *et al.*, 2008; Cheng, 2008; Ikawa *et al.*, 2012b; Nakajo *et al.*, 2013; Ikawa *et al.*, 2013; Harada *et al.*, 2016; Ung *et al.*, 2016; Furuki *et al.*, 2017.

Notes. Records provided by Esaki (1928a, 1930a, 1932, 1933, 1937b, 1950), Wu (1935), Yamada (1939), Takara (1957), Chen & Andersen (1993), Chen *et al.* (1993), and Hua (2000) are erroneous. Usinger (1938), Hoffmann (1941), and Poisson (1965) mistakenly considered *H. alluaudi* and *H. matsumurai* synonyms of *H. princeps*, which was first proposed by Esaki (1928a). According to Zettel (2005), the record from Penang, Malaysia, provided by Herring (1961) [and repeated by Andersen & Foster, 1992] is probably based on a female of *H. esakii*.

Halobates proavus White, 1883

Halobates proavus White, 1883: 54. – HT: ♂, Indonesia (Moluccas Arch.), Halmahera, "Gilolo" [Jailolo]; BMNH.

DISTRIBUTION. **OR:** Andaman Sea, Christmas Is., India (Nicobar Is.), Indonesia (Java Is., Moluccas Arch., Sulawesi Is.), Malaysia (Kedah, Pahang, Penang, Selangor, Tioman Is.), Philippines (Catanduanes Is.!, Cebu Is., Luzon Is., Mindanao Is., Mindoro Is.!), Singapore, Thailand (Phuket); **AU:** Papua New Guinea (D'Entrecasteaux Is., Milne Bay, Morobe), Solomon Islands (New Georgia Is.), Vanuatu (Espiritu Santo Is.).

Ref.: Girard, 1885; Dahl, 1893; Lethierry & Severin, 1896; Kirby, 1900; Esaki 1930b; 1933; Imms, 1936; Izzard, 1936; Usinger, 1938; Matsuda, 1960; Herring, 1961; Cheng & Fernando, 1969; Fernando & Cheng, 1974; Gross, 1975; Cheng, 1985; 1989; Andersen & Foster, 1992; Yang *et al.*, 1999; Damgaard *et al.*, 2000; Cheng *et al.*, 2001; Andersen, 2001; Thirumalai, 2002; Andersen & Cheng, 2004; Radhakrishnan & Thirumalai, 2004; Nieser & Chen, 2005; Chen *et al.*, 2005; J. T. Polhemus & D. A. Polhemus, 2006; D. A. Polhemus *et al.*, 2008; Cheng, 2008; Zettel & Tran, 2009; Sites & Vitheepradit, 2010; Chandra *et al.*, 2012; Ikawa *et al.*, 2012b; Balakrishnan *et al.*, 2012; Zettel, 2014; Palacios & Lopez, 2015; Bendanillo *et al.*, 2016.

Notes. Records from the Red Sea are based on misidentifications. Ikawa *et al.* (2012b) mistakenly listed the species from Australia. First records from the Philippine islands of Catanduanes and Mindoro are based on specimens deposited in the NHMW and the UPLB.

Halobates regalis Carpenter, 1892

Halobates regalis Carpenter, 1892: 144. – HT: ♂, Australia, Torres Strait; BMNH.

DISTRIBUTION. **AU:** Australia (Queensland, Western Australia).

Ref.: Hale, 1925; Walker, 1893a; Lethierry & Severin, 1896; Esaki, 1933; Usinger, 1938; China, 1957; Herring, 1961; Cheng, 1985; 1989; Malipatil, 1988; Cheng, 1989; Andersen, 1991a; 1991b; Andersen & Weir, 1994b; Cassis & Gross, 1995; Andersen, 1998a; Turner *et al.*, 2001; Andersen & Cheng, 2004; Andersen & Weir, 2004; Chen *et al.*, 2005; Cheng, 2008; Ikawa *et al.*, 2012b; Ung *et al.*, 2016.

Halobates rivularis (Andersen & Weir, 1994)

Austrobates rivularis Andersen & Weir, 1994a: 6. – HT: ♂, Australia, Queensland, Lydia Creek; ANIC.
Halobates rivularis (Andersen & Weir, 1994) (**new combination**).

DISTRIBUTION. **AU:** Australia (Queensland).

Ref.: Cassis & Gross, 1995; Andersen & Cheng, 2004; Andersen & Weir, 2004.

Halobates robinsoni Andersen & Weir, 2003

Halobates robinsoni Andersen & Weir, 2003: 11. – HT: ♂, Australia, Western Australia, Lower Robinson, Robinson River; ANIC.

DISTRIBUTION: **AU:** Australia (Western Australia).

Ref.: Andersen & Cheng, 2004; Andersen & Weir, 2004; J. T. Polhemus & D. A. Polhemus, 2008; Cheng, 2008; Ikawa *et al.*, 2012b.

Halobates robustus Barber, 1925

Halobates robustus Barber, 1925: 253. – ST: ♀♂, Galapagos Islands; AMNH. AQ12

DISTRIBUTION: **NR:** Ecuador (Galapagos Is.).

Ref.: Esaki, 1933; Barber, 1934; Usinger, 1938; Herring, 1961; Linsley & Usinger, 1966; Jaczewski, 1972; Cheng *et al.*, 1979; Birch *et al.*, 1979; Schulz-Baldes & Cheng, 1979; Cheng & Maxfield, 1980; Foster & Treherne, 1980; Schulz-Baldes & Cheng, 1981; Froeschner, 1981; Foster & Treherne, 1982; Newman & Cheng, 1983; Froeschner, 1985; Cheng, 1985; 1989; Andersen, 1991a; Damgaard *et al.*, 2000; Peck, 2001; Andersen, 2001; Danulat & Edgar, 2002; Andersen & Cheng, 2004; Cheng, 2008; Buzzetti & Cianferoni, 2011; Cheng *et al.*, 2011; Ikawa *et al.*, 2012b; Palacios & Lopez, 2015; Moreira, 2015; Fairbairn *et al.*, 2016.

†***Halobates ruffoi*** Andersen, Farma, Minelli & Piccoli, 1994

†*Halobates ruffoi* Andersen, Farma, Minelli & Piccoli, 1994: 480–483, figs 1–2. – HT: ♀, Italy, Verona, Pesciara di Bolca deposit; MCVR.

DISTRIBUTION: **PA:** Italy (Pesciara di Bolca deposit, about 45 Mya).

Halobates salotae Herring, 1961

Halobates salotae Herring, 1961: 260. – HT: ♂, Tonga, "Tongatabu" [Tongatapu]; BPBM.

DISTRIBUTION: **AU:** Tonga (Tongatapu Is., Vava'u Is.).

Ref.: J. T. Polhemus & Cheng, 1982; Cheng, 1985; 1989; Andersen, 1991b; Andersen, 1998a; Damgaard *et al.*, 2000; Cheng, 2008; Ikawa *et al.*, 2012b; Palacios & Lopez, 2015; Ung *et al.*, 2016.

Halobates sericeus Eschscholtz, 1822

Halobates sericeus Eschscholtz, 1822: 108, pl. 2, fig. 4. – ST: ♀♂, North Pacific; IZBE. AQ13

DISTRIBUTION. Pacific Ocean between 40–45° N and 40° S; **AS:** China, Japan; Taiwan; **OR:** Indonesia, Vietnam; **AU:** Australia, Hawaiian Is., Johnston Atoll, Marshall Is., New Caledonia, New Zealand, Papua New Guinea, Vanuatu; **NA:** United States of America; **NR:** Chile, Colombia, Ecuador (including Galapagos Is.), Mexico, Peru.

Ref.: Laporte, 1832; Burmeister, 1835; Spinola, 1837; Blanchard, 1840; White, 1883; Witlaczil, 1886; Dahl, 1893; Walker, 1893a; Fritze, 1894; Lethierry & Severin, 1896; Matsumura, 1900; Alfken, 1903; Oshanin, 1908; Kirkaldy, 1908; Kirkaldy & Torre-Bueno, 1909; Kirkaldy, 1910a; Banks, 1910; Oshanin, 1912; Matsumura, 1913; Lundbeck, 1914; Van Duzee, 1916; 1917; Myers, 1921; Bryan, 1922; Esaki, 1924; 1926a; Bryan & Swezey, 1926; Myers, 1926; Matsumura, 1930; 1931; 1932; Esaki, 1933; Hoffmann, 1933; De Carlo, 1935; Wu, 1935; Imms, 1936; Usinger, 1938; Hoffmann, 1941; Barber, 1943; Williams, 1944; Edmondson, 1946; Zimmermann, 1948; Esaki, 1950; Jordan, 1952; Chilson, 1953; Usinger & Herring, 1957; Miyamoto, 1957; Herring, 1958; Miyamoto & Senta, 1960; Matsuda, 1960; Herring, 1961; Miyamoto, 1961a; 1962; Wise, 1965; Cheng, 1971; Weidner, 1972; Cheng, 1972; 1973a; Lee & Cheng, 1974; Cheng, 1975; Andersen & J. T. Polhemus, 1976; Cheng *et al.*, 1978; Tomokuni & Sato, 1978; J. T. Polhemus & Chapman, 1979; Cheng & Schulenberger, 1980; Cheng & Hill, 1980; Froeschner, 1981; Casale, 1981; Andersen, 1981; 1982; J. T. Polhemus & Cheng, 1982; Cheng & Schmitt, 1982; Springer, 1982; Cheng & Holdway, 1983; Cheng & Harrison, 1983; Cheng *et al.*, 1984; Cheng, 1985; Froeschner, 1985; Harrison & Seki, 1987; Malipatil, 1988; Henry & Froeschner, 1988; Cheng, 1989; Andersen, 1991a; Chen & Andersen, 1993; Chen *et al.*, 1993; Senta *et al.* 1993; Andersen & Weir, 1994b; Aukema & Rieger, 1995; Cheng & Holdway, 1995; Cassis & Gross, 1995; J. T. Polhemus, 1996; Seapy, 1996; Cheng, 1997; Andersen, 1998a; Ikawa *et al.*, 1998; Froeschner, 1999; Chen, 1999; Hua, 2000; Damgaard *et al.*, 2000; Muraji & Tachikawa, 2000; Andersen *et al.*, 2000; Peck, 2001; Nakatani, 2001; Andersen, 2001; Aristizábal, 2002; Ikawa *et al.*, 2002; Cheng & Mathis, 2003; Larivière & Larochelle, 2004; Andersen & Cheng, 2004; Andersen & Weir, 2004; Ikawa *et al.*, 2004; Harada, 2005; Damgaard *et al.*, 2005; J. T. Polhemus & D. A. Polhemus, 2006; Cheng, 2006; 2008; Prado, 2008; Cheng *et al.*, 2010; 2011; Buzzetti & Cianferoni,

2011; Harada *et al.*, 2011a; 2011b; Yamada & Hama, 2012; Goldstein *et al.*, 2012; Leo *et al.*, 2012; Ikawa *et al.*, 2012b; Fraval, 2012; Ôhara *et al.*, 2013; Nakajo *et al.*, 2013; Sekimoto *et al.*, 2013; Harada *et al.*, 2013; Matsuda & Kawano, 2014; Engels *et al.*, 2014; Damgaard & Zettel, 2014; Larivière & Larochelle, 2014; Palacios & Lopez, 2015; Umamoto *et al.*, 2015; Zhou *et al.*, 2015; Kiessling *et al.*, 2015; ECCIJ, 2016; Furuki *et al.*, 2016; Harada *et al.*, 2016; 2017; Furuki *et al.*, 2017.

Note. Records from out of the Pacific Ocean are erroneous.

Halobates sexualis Distant, 1903

Halobates sexualis Distant, 1903b: 258. – HT: ♂, [Thailand, Pattani], estuary of the Jambu River, Jhering; BMNH.

DISTRIBUTION. **OR:** Malaysia (Kedah), Sri Lanka (North Western, Western), Thailand (Pattani, Phatthalung).

Ref.: Paiva, 1917; Esaki, 1933; Usinger, 1938; Herring, 1961; Cheng, 1985; 1989; Andersen, 1991a; 1991b; Andersen & Foster, 1992; Andersen, 1998a; Damgaard *et al.*, 2000; Andersen, 2001; Cheng *et al.*, 2001; Andersen & Cheng, 2004; Chen *et al.*, 2005; Cheng, 2008; Zettel & Tran, 2009; Ikawa *et al.*, 2012b; Palacios & Lopez, 2015; Ung *et al.*, 2016.

Note. According to the itinerary and map provided by Annandale & Robinson (1903), the type locality of this species is in southern Thailand, not in northern Malaysia as commonly considered in the literature. The only existing record truly from Malaysia was provided by Zettel & Tran (2009).

Halobates sobrinus White, 1883

Halobates sobrinus White, 1883: 46, pl. 1, fig. 5. – HT: ♂, Society Islands, Tahiti [probably an error; see Herring, 1961: 252]; NHRS.

DISTRIBUTION. East Pacific Ocean between 30° N and 5° S; **NA:** United States of America; **NR:** Clipperton Is., Colombia, Costa Rica, Ecuador (including Galapagos Is.), El Salvador, Guatemala, Mexico, Nicaragua, Panama, Peru.

Ref.: Girard, 1885; Dahl, 1893; Walker, 1893a; Lethierry & Severin, 1896; Kirkaldy & Torre-Bueno, 1909; Esaki, 1933; Usinger, 1938; Herring, 1958; Matsuda, 1960; Herring, 1961; Linsley & Usinger, 1966; Weidner, 1972; Jaczewski, 1972; Cheng, 1973a; 1975; Andersen & J. T. Polhemus, 1976; Cheng & Schulenberger, 1980; Froeschner, 1981; Andersen, 1982; Cheng & Holdway, 1983; Froeschner, 1985; Cheng, 1985; 1989; Andersen, 1991a; Cheng & Holdway, 1995; Andersen, 1998a; Ikawa *et al.*, 1998; Froeschner, 1999; Damgaard *et al.*, 2000; Andersen *et al.*, 2000; Peck, 2001; Andersen, 2001; Aristizábal, 2002; Cheng & Pitman, 2002; Danulat & Edgar, 2002; Petrakis *et al.*, 2003; Andersen & Cheng, 2004; Molano-Rendón *et al.*, 2005; Cheng, 2006; Posso & González, 2008; Molano-Rendón *et al.*, 2008; Cheng, 2008; Garrouste & Cheng, 2009; Cheng *et al.*, 2010; 2011; Buzzetti & Cianferoni, 2011;

Harada *et al.*, 2011b; Ikawa *et al.*, 2012b; Cheng *et al.*, 2012; Engels *et al.*, 2014; Palacios & Lopez, 2015; Padilla-Gil, 2015.

Halobates splendens Witlaczil, 1886

AQ14 *Halobates splendens* Witlaczil, 1886: 178. – ST: ♀♂, Pacific Ocean on the west coast of America between the Equator and the Tropic of Capricorn; NHMW?.

Halobates streatfieldanus var. *magentae* Griffini, 1895: 4 (syn. Herring, 1961: 248). –
AQ15 ST: ♀♂ Pacific Ocean, "Mare di Valparaiso" and "Mare del Chili"; MIZT.

DISTRIBUTION. Southeast Pacific Ocean between 15° N and 30° S; **NR:** Chile, Colombia, Costa Rica, Ecuador (including Galapagos Is.), Peru.

Ref.: Dahl, 1893; Walker, 1893b; Lethierry & Severin, 1896; Esaki, 1933; Usinger, 1938; Barber, 1943; Matsuda, 1960; Weidner, 1972; Jaczewski, 1972; Cheng, 1973a; 1975; Cheng & Schulenberger, 1980; Froeschner, 1981; Andersen, 1982; Cheng & Holdway, 1983; Froeschner, 1985; Cheng, 1985; 1989; Andersen, 1991a; Cheng & Holdway, 1995; Andersen, 1998a; Ikawa *et al.*, 1998; Damgaard *et al.*, 2000; Andersen *et al.*, 2000; Peck, 2001; Andersen, 2001; Aristizábal, 2002; Andersen & Cheng, 2004; Molano-Rendón *et al.*, 2005; Cheng, 2006; Posso & González, 2008; Prado, 2008; Molano-Rendón *et al.*, 2008; Cheng, 2008; Ferrú & Sielfeld, 2010; Buzzetti & Cianferoni, 2011; Cheng *et al.*, 2010; 2011; Harada *et al.*, 2011b; Cheng *et al.*, 2012; Ikawa *et al.*, 2012b; Engels *et al.*, 2014; Palacios & Lopez, 2015; Padilla-Gil, 2015.

Halobates tethys Herring, 1961

Halobates tethys Herring, 1961: 273. – HT: ♂, Mauritius, Pointe aux Sables; SEMC.

DISTRIBUTION. Mauritius (Port Louis, Rivière Noire).

Ref.: Cheng, 1985; 1989; Andersen, 1991b; Andersen & Foster, 1992; Andersen, 1998a; Andersen & Cheng, 2004; D. A. Polhemus & J. T. Polhemus, 2008; Cheng, 2008; Ikawa *et al.*, 2012b.

Halobates trynae Herring, 1964

Halobates trynae Herring, 1964: 85. – HT: ♂, Bay of Bengal, 6° 19' N, 92° E; USNM.

DISTRIBUTION. **OR:** India (Bay of Bengal, Nicobar Is.), Malaysia (Negeri Sembilan), Thailand (Phuket), Singapore.

Ref.: Cheng, 1985; Andersen & Foster, 1992; Cheng *et al.*, 2001; Thirumalai, 2002; Andersen & Cheng, 2004; Radhakrishnan & Thirumalai, 2004; Chen *et al.*, 2005; Cheng, 2008; Chandra *et al.*, 2012; Ikawa *et al.*, 2012b; Balakrishnan *et al.*, 2012.

Halobates whiteleggei Skuse, 1891

AQ16 *Halobates whiteleggei* Skuse, 1891: 174. – HT: ♀♂, Australia, New South Wales, Port Jackson; AMS.

DISTRIBUTION. **AU:** Australia (New South Wales, Queensland).

Ref.: Skuse, 1893; Walker, 1893a; Lethierry & Severin, 1896; Esaki, 1933; Usinger, 1938; Herring, 1961; Cheng, 1985; Malipatil, 1988; Cheng, 1989; Andersen, 1991a; 1991b; Andersen & Weir, 1994b; Cassis & Gross, 1995; Andersen, 1998a; Damgaard *et al.*, 2000; Andersen, 2001; Andersen & Cheng, 2004; Andersen & Weir, 2004; Cheng, 2008; Ikawa *et al.*, 2012b; Ung *et al.*, 2016.

Halobates zephyrus Herring, 1961

Halobates zephyrus Herring, 1961: 276. – HT: ♂, Australia, Queensland, Bribie Island; USNM.

DISTRIBUTION. **AU:** Australia (New South Wales, Queensland).

Ref.: J. T. Polhemus & Cheng, 1982; Cheng, 1985; Malipatil, 1988; Cheng, 1989; Andersen, 1991a; 1991b; Andersen & Weir, 1994b; Cassis & Gross, 1995; Andersen, 1998a; Andersen & Cheng, 2004; Andersen & Weir, 2004; Cheng, 2008; Ikawa *et al.*, 2012b; Ung *et al.*, 2016.

Tribe Metrocorini Matsuda, 1960 (7 genera, 126 species, 3 subgenera, 4 subspecies)

Genus ***Esakia*** Lundblad, 1933 (10 species)

Esakia Lundblad, 1933: 9, 19, 404, 455–456, 459, 463, 466, 469, tab. 4, tab. 6, plt. 12 (correct original spelling chosen by first revisers, Hungerford & Matsuda, 1958). – Type species by monotypy: *Esakia ventidioides* Lundblad, 1933.
Esakiella Lundblad, 1933: 401, 405 (incorrect original spelling; non *Esakiella* China, 1932).

Esakia cenizae Zettel, 2004

Esakia cenizae Zettel, 2004: 382. – HT: ♂, Philippines, Bohol, NE Tagbilaran, S Sikatuna, near Dangay; UPLB.

DISTRIBUTION. **OR:** Philippines (Bohol Is., Samar Is.).

Ref.: Chen *et al.*, 2005; Suksai *et al.*, 2015.

Esakia fernandoi Cheng, 1966

Esakia fernandoi Cheng, 1966: 16. – HT: ♂, Malaysia, Johor, Mupoh River; BMNH.
Esakia fernanndoi; Chen & Zettel, 1999b: 139 (incorrect subsequent spelling).

DISTRIBUTION. **OR:** Malaysia (Johor), Singapore.

Ref.: Cheng & Fernando, 1969; Fernando & Cheng, 1974; J. T. Polhemus, 1992; Cheng *et al.*, 2001; Chen *et al.*, 2005; Suksai *et al.*, 2015.

Note. See *E. hungerfordi*.

***Esakia hungerfordi* Miyamoto, 1967**

Esakia hungerfordi Miyamoto, 1967: 251. – HT: ♂, Brunei, Rambai; KUEC.

DISTRIBUTION. **OR:** Brunei (Tutong).

Ref.: J. T. Polhemus, 1992; Suksai *et al.*, 2015.

Note. After studies of topotypical specimens from Johor and Brunei, the synonymy of *E. fernandoi* and *E. hungerfordi* proposed by J. T. Polhemus (1992) is rejected (Tran A.D. & H. Zettel, in prep.).

Esakia johorensis Cheng, 1966

Esakia johorensis Cheng, 1966: 18. – HT: ♂, Malaysia, Johor, Johore Bahru-Sedili road; BMNH.

DISTRIBUTION. **OR:** Malaysia (Johor).

Ref.: Cheng & Fernando, 1969; Fernando & Cheng, 1974; Cheng *et al.*, 2001; Chen *et al.*, 2005; Suksai *et al.*, 2015.

Esakia kuiterti Hungerford & Matsuda, 1958

Esakia kuiterti Hungerford & Matsuda, 1958: 193. HT: ♂, "Burma" [Myanmar], Tingkawk; SEMC.

DISTRIBUTION. **OR:** Myanmar (Kachin).

Ref.: Matsuda, 1960; J. T. Polhemus, 1992; Suksai *et al.* (2015).

Note. The synonymy with *E. ventidioides* by J. T. Polhemus (1992) is rejected as there are – besides the geographical distance – clear morphological differences in the original descriptions of the two taxa (Tran A.D. & H. Zettel, in prep.).

Esakia latonota Tran & Zettel, 2013

Esakia latonota Tran & Zettel, 2013: 22. – HT: ♂, Vietnam, Nam Cat Tien N. P.; NHMW.

DISTRIBUTION. **OR:** Vietnam (Đồng Nai), Thailand (Loei).

Ref.: Suksai *et al.*, 2015; 2016.

Esakia lundbladi Cheng, 1966

Esakia lundbladi Cheng, 1966: 20. – HT: ♂, Malaysia, Johor, Sedili Ulu River; BMNH.

DISTRIBUTION. **OR:** Malaysia (Johor).

Ref.: Cheng & Fernando, 1969, Fernando & Cheng, 1974; Cheng *et al.*, 2001; Chen *et al.*, 2005; Suksai *et al.*, 2015.

Esakia palawanensis Zettel, 2004

Esakia palawanensis Zettel, 2004: 379. – HT: ♂, Philippines, Palawan, Tacduan area, Tacduan River; NHMW.

DISTRIBUTION. **OR:** Philippines (Busuanga Is., Palawan Is.).

Ref.: Chen *et al.*, 2005; Freitag & Zettel, 2012; Suksai *et al.*, 2015.

Esakia usingeri Hungerford & Matsuda, 1958

Esakia usingeri Hungerford & Matsuda, 1958: 196. – HT: ♂, Philippines, Luzon, Rizal Province, Montalban; CASC.

DISTRIBUTION. **OR:** Philippines (Luzon Is.).

Ref.: Matsuda, 1960; Zettel, 2004; Chen *et al.*, 2005; Zettel, 2014; Suksai *et al.*, 2015.

Esakia ventidioides Lundblad, 1933

Esakia ventidioides Lundblad, 1933: 401. – HT: ♂, Indonesia, Sumatra (South), Musi area, Tjurup; NHRS.
Esakia ventitoides; J. T. Polhemus, 1992: 440 (incorrect subsequent spelling).

DISTRIBUTION. **OR:** Indonesia (Sumatra Is.).

Ref.: Matsuda, 1960; J. T. Polhemus, 1992; Chen & Nieser, 1992; Chen & Zettel, 1999b; Chen *et al.*, 2005; Zettel, 2011a; Suksai *et al.*, 2015.

Note. See *E. kuiterti*.

Genus ***Eurymetra*** Esaki, 1926 (7 species, 4 subspecies)

Metrocoris (*Eurymetra*) Esaki, 1926a: 129. – Type species by original designation: *Metrocoris natalensis* Distant, 1903.
Eurymetra Esaki, 1926 (as genus); Esaki, 1928b: 512.
Cesametra Koçak & Kemal, 2009: 4 (unnecessary replacement name; *Eurymetra* Odhner, 1910 is a *nomen nudum*; see Poche, 1925: 133).

Eurymetra aethiops (Distant, 1903)

Metrocoris aethiops Distant, 1903c: 472. – ST: ♂♀, Nigeria, Abutsi River; BMNH.
Metrocoris (*Eurymetra*) *aethiops* Distant, 1903; Esaki, 1926a: 129.
Eurymetra aethiops (Distant, 1903); Esaki, 1928b: 512.

DISTRIBUTION: **AF:** Burkina Faso (Cascades, Hauts-Bassins), Cameroon (Centre), Central African Republic (Lobaye), D. R. Congo (Haut-Katanga), Guinea (Kindia, Nzérékoré), Ivory Coast (Montagnes), Nigeria.

Ref.: Esaki, 1926a; Poisson, 1929; 1940; 1945; 1954b; 1955a; Hoberlandt, 1958; Poisson, 1960a; 1965; Dethier, 1981; Linnavuori, 1981.

Eurymetra africana Poisson, 1947

Eurymetra africana Poisson, 1947: 11. – HT: ♀, Ivory Coast, Réserve de Banco; repository unknown.

DISTRIBUTION. **AF:** Equatorial Guinea!, Cameroon (Ouest, Sud-Ouest), Ghana (Ashanti), Ivory Coast (Abidjan), Liberia!, Nigeria (Ondo, Osun).

Ref.: Poisson, 1948; Linnavuori, 1981.

Notes. Treated as a synonym of *E. aethiops* by Poisson (1955a; 1965), but not by Linnavuori (1981), a decision that is followed here. First records from Equatorial Guinea and Liberia are based on specimens deposited in the NHMW.

Eurymetra angolensis Hoberlandt, 1951

Eurymetra angolensis Hoberlandt, 1951: 11. – HT: ♂, Angola, Brook Kamassangu, 85 km SSE of Dundo; MD.
Eurymetra natalensis angolensis Hoberlandt, 1951; Linnavuori, 1971: 360.
Eurymetra angolensis Hoberlandt, 1951 (**status restored**).

DISTRIBUTION. **AF:** Angola (Lunda Norte), Cameroon (Est), Guinea (Nzérékoré), Central African Republic (Ombella-M'Poko), D. R. Congo (Haut-Katanga, Haut-Lomami, Haut-Uele), South Sudan (Imatong, Yei River), Uganda!, Zambia (Luapula, Muchinga).

Ref.: Poisson, 1954a; 1954b; Matsuda, 1960; Poisson, 1964; 1965; 1968; Poisson & Sallier Dupin, 1969; Linnavuori, 1971; 1981; Kment & Kolínová, 2013.

Notes. Considering the distinct morphological differences and the wide overlap in the geographic distribution of *E. natalensis* and *E. angolensis*, the subspecific status of the latter proposed by Linnavuori (1971) is rejected. The first record from Uganda is based on specimens deposited in the NHMW.

Eurymetra madagascariensis Poisson, 1945

Eurymetra madagascariensis Poisson, 1945: 89. – ST: 2♀♀, Madagascar; MNHN.

DISTRIBUTION. **AF:** Madagascar.

Ref.: Poisson, 1965; Fossati, 2001.

Eurymetra natalensis natalensis (Distant, 1903)

Metrocoris natalensis Distant, 1903c: 473. – ST: ♀♀, South Africa, Natal, Pirie Bush; BMNH.
Metrocoris distanti Kirkaldy, 1904: 62 (syn. Esaki, 1926a: 128). – HT: ♀, South Africa, Zoutspanberg; BMNH.
Metrocoris (*Eurymetra*) *natalensis* Distant, 1903; Esaki, 1926a: 128–129.
Eurymetra natalensis (Distant, 1903); Esaki, 1928b: 512.

Eurymetra natalensis natalensis (Distant, 1903); Linnavuori, 1971: 360.

DISTRIBUTION. **AF:** Cameroon (Ouest); Central African Republic (Ombella-M'Poko/Ouham), D. R. Congo (Haut-Katanga, Haut-Uele), Ethiopia (Addis Abeba, Oromia, Southern Nations, Nationalities, and Peoples), Guinea (Nzérékoré), Kenya (Kiambu, Laikipia, Nairobi, Nyeri, Uasin Gishu), Lesotho (Maseru), Rwanda (Sud), South Africa (Eastern Cape, KwaZulu-Natal, Limpopo, Mpumalanga, Western Cape), South Sudan (Imatong), Tanzania (Kilimanjaro, Tanga), Uganda (Eastern, Western), Zambia (Central), Zimbabwe (Midlands).

Ref.: Kirkaldy, 1910b; Bergroth, 1914; Poisson, 1941; 1948; 1952; 1954a; 1954b; Hynes, 1955; Poisson, 1955b; 1955c; 1957; 1960b; Matsuda, 1960; Mancini, 1961; Poisson, 1963; 1964; 1965; 1968; Poisson & Sallier Dupin, 1969; Linnavuori, 1971; 1981; Nummelin, 1988; Mwabvu & Sasa, 2009; Snaddon, 2009.

Eurymetra natalensis fallaciosa Linnavuori, 1981

Eurymetra natalensis fallaciosa Linnavuori, 1981: 15. – HT: ♂, Togo, near Agbaudi; AMNH.

DISTRIBUTION. **AF:** Burkina Faso (Cascades), Togo (Plateaux).

Eurymetra nitidula nitidula (Esaki, 1926)

Metrocoris (*Eurymetra*) *nitidulus* Esaki, 1926a: 126. – ST: ♀♂, "Abyssinia" [Ethiopia], Lake Abasse; HNHM. AQ17
Eurymetra nitidula (Esaki, 1926); Esaki, 1928b: 512.
Eurymetra nitidula nitidula (Esaki, 1926); Poisson, 1940: 5.

DISTRIBUTION. **AF:** D. R. Congo (Haut-Katanga), Ethiopia (Oromia).

Ref.: Matsuda, 1960; Poisson, 1965; Poisson & Sallier Dupin, 1969; Linnavuori, 1981.

Eurymetra nitidula aethiopica Poisson, 1940

Eurymetra aethiopica Poisson, 1940: 5. – HT: ♀, Ethiopia, Goba; ISNB
Eurymetra nitidula aethiopica Poisson, 1940; Poisson, 1965: 1499.

DISTRIBUTION. **AF:** Ethiopia (Oromia).

Ref.: Linnavuori, 1981.

Eurymetra pauliani Poisson, 1941

Eurymetra pauliani Poisson, 1941: 15. – ST: 5♀♀, Cameroon, Mt. N'Lonako, N'Kongsamba; MNHN.

DISTRIBUTION. **AF:** Cameroon (Littoral), Nigeria (Cross River, Taraba).

Ref.: Villiers, 1952; Poisson, 1965; Linnavuori, 1981.

Genus ***Eurymetropsiella*** Poisson, 1950 (3 species)

Eurymetropsiella Poisson, 1950: 73. – Type species by original designation and monotypy: *Eurymetropsiella schoutedeni* Poisson, 1950.

Eurymetropsiella congoensis Poisson, 1955

Eurymetropsiella congoensis Poisson, 1955d: 156. – ST: 1♂, 1♀, Congo, Brazzaville; USNM.

DISTRIBUTION. **AF:** Congo (Brazzaville).

Ref.: Poisson, 1965.

Eurymetropsiella manengolensis (Hoberlandt, 1950)

Eurymetra manengolensis Hoberlandt, 1950: 1. – HT: ♀, Cameroon (West), Manengole; NMPC.
Eurymetropsiella manengolensis (Hoberlandt, 1950); Linnavuori, 1981: 15.

DISTRIBUTION. **AF:** Cameroon (Littoral), Central African Republic (Ombella-M'Poko).

Ref.: Poisson, 1965; Linnavuori, 1981; Dethier, 1981; Kment & Kolínová, 2013; Tchakonté *et al.*, 2015.

Eurymetropsiella schoutedeni Poisson, 1950

Eurymetropsiella schoutedeni Poisson, 1950: 74. – ST: ♂♀, D. R. Congo, Kibali Ituri, Dramba; MRAC.

DISTRIBUTION. **AF:** Benin (Atakora), D. R. Congo (Haut-Uele), Nigeria (Taraba).

Ref.: Poisson, 1951; Matsuda, 1960; Poisson, 1965; Linnavuori, 1981.

Genus ***Eurymetropsielloides*** Poisson, 1956 (1 species)

Eurymetropsielloides Poisson, 1956: 246. – Type species by monotypy: *Eurymetropsielloides milloti* Poisson, 1956.

Eurymetropsielloides milloti Poisson, 1956

Eurymetropsielloides milloti Poisson, 1956: 246. – HT: ♂, Madagascar, Moramanga, Sandrangato; USNM.

DISTRIBUTION. **AF:** Madagascar (Alaotra-Mangoro).

Ref.: Poisson, 1965.

Genus ***Eurymetropsis*** Poisson, 1948 (2 species)

Eurymetropsis Poisson, 1948: 169. – Type species by original designation and monotypy: *Eurymetropsis carayoni* Poisson, 1948.

Eurymetropsis carayoni Poisson, 1948

Eurymetropsis carayoni Poisson, 1948: 169. – ST: ♂♀, Cameroon, N'tchi; MNHN.

DISTRIBUTION. **AF:** Cameroon (Ouest), Nigeria (Cross River, Taraba).

Ref.: Matsuda, 1960; Poisson, 1965; Linnavuori, 1981; Dethier, 1981.

Eurymetropsis umbrina Linnavuori, 1981

Eurymetropsis umbrina Linnavuori, 1981: 16. – HT: ♂, Cameroon, Mount Cameroon, Buea; AMNH.

DISTRIBUTION. **AF:** Cameroon (Sud-Ouest).

Genus ***Metrocoris*** Mayr, 1865 (80 species)

Metrocoris Mayr, 1865: 445. – Type species by monotypy: *Halobates brevis* Mayr, 1865 [= *Halobates stali* Dohrn, 1860].
Halobatodes White, 1883: 23, 58 (syn. Meinert, 1888: 140). – Type species by original designation: *Halobates lituratus* Stål, 1854.
Gerastratus Distant, 1910a: 148 (syn. Esaki, 1929: 417). – Type species by monotypy: *Gerastratus foveatus* Distant, 1910.
Euodus Distant, 1910a: 150 (syn. Esaki, 1929: 418). – Type species by monotypy: *Euodus communis* Distant, 1910.
Metrocoropsis Paiva, 1919: 365 (syn. Esaki, 1926a: 129–130). – Type species by original designation and monotypy: *Metrocoropsis femorata* Paiva, 1919.

Metrocoris acutus Chen & Nieser, 1993

Metrocoris acutus Chen & Nieser, 1993a: 32. – HT: ♂, Thailand, Chiang Mai, Konthanthan Waterfall [probable misspelling for Mon Tha Than Waterfall]; ZMUC.

DISTRIBUTION. **AS:** China (Yunnan); **OR:** Laos (Luang Prabang), Thailand (Chiang Mai, Kanchanaburi, Mae Hong Son, Phetchabun), Vietnam (Bắc Kạn, Bắc Thái, Cao Bằng, Điện Biên, Hà Giang, Hà Nội, Hà Sơn Bình, Hà Tĩnh, Hải Hưng, Hải Dương, Hòa Bình, Lai Châu, Lào Cai, Nghệ An, Ninh Bình, Phú Thọ, Quảng Ninh, Sơn La, Thanh Hóa, Vĩnh Phúc).

Ref.: Chen & Andersen, 1993; Chen *et al.*, 1993; Chen, 1994; Aukema *et al.*, 1995; Zettel & Chen, 1996; Chen & Zettel, 1998; Cheng *et al.*, 2006; Chen *et al.*, 2006b; Hutacharern *et al.* 2007; Lekprayoon *et al.*, 2007; Tran & D. A. Polhemus, 2017.

Metrocoris anderseni Chen & Nieser, 1993

Metrocoris anderseni Chen & Nieser, 1993a: 23. – HT: ♂, India, Uttar Pradesh [Uttarakhand], Naini Tal [Nainital], Haldwani; ZMUC.

DISTRIBUTION. **OR:** India (Uttarakhand).

Ref.: Thirumalai, 2002; Basu *et al.*, 2016a.

Notes. Originally recorded from two localities in Uttar Pradesh State (India) that are part of Uttarakhand State since its establishment in November, 2000. Listed from West Bengal, India, by Basu *et al.* (2016a), but original record could not be found.

Metrocoris angustus Chen & Nieser, 1993

Metrocoris angustus Chen & Nieser, 1993b: 63. – HT: ♂, "Burma" [Myanmar], "Bumgahtaung-Hpungan"; NHRS.

DISTRIBUTION: **OR:** Myanmar (Kachin).

Ref.: Zettel, 2011a.

Metrocoris armatus Chen & Nieser, 1993

Metrocoris armatus Chen & Nieser, 1993a: 14. – HT: ♂, Thailand, Loei Province, Phu Luang Wildlife Sanctuary; ZMUC.

DISTRIBUTION. **OR:** Thailand (Chayaphum!, Loei, Phetchabun!).

Ref.: Chen & Zettel, 1998; Hutacharern *et al.* 2007; Tran & D. A. Polhemus, 2017.

Note. First province records are based on specimens deposited in the NHMW.

Metrocoris astictus Ye, Chen & Bu, 2016

Metrocoris astictus Ye, Chen & Bu, 2016: 368. – HT: ♂, China, Sichuan Prov., Luzhou city, Xuyong county, Huagaoxi Nature Reserve; NKUM.

DISTRIBUTION. **OR:** China (Sichuan).

Metrocoris atlas Zettel, 2011

Metrocoris atlas Zettel, 2011a: 105. – HT: ♂, Myanmar, Sagaing Division [Region], Alaungdaw Katthapa National Park, Khaung Din Stream; NHMW.

DISTRIBUTION. **OR:** Myanmar (Sagaing).

Metrocoris bilobatoides Chen & Nieser, 1993

Metrocoris bilobatoides Chen & Nieser, 1993a: 20. – HT: ♂, Vietnam, Vĩnh Phúc, Tam Đảo; NHRS.

DISTRIBUTION. **OR:** Vietnam (Hà Giang, Hà Sơn Bình, Lào Cai, Ninh Bình, Vĩnh Phúc).

Ref.: Zettel & Chen, 1996; Tran & D. A. Polhemus, 2017.

Metrocoris bilobatus Boer, 1965

Metrocoris bilobatus Boer, 1965: 15. – HT: ♀, China, Yunnan, Yunnan-Fou, "San-nen-kai" [Sannankai]; RMNH.

DISTRIBUTION. **AS:** China (Yunnan).

Ref.: Chen & Nieser, 1993a; Chen & Andersen, 1993; Chen *et al.*, 1993; Chen, 1994; Aukema & Rieger, 1995; Hua, 2000; Cheng *et al.*, 2006; Tran & D. A. Polhemus, 2017.

Metrocoris borneensis D. A. Polhemus, 1990

Metrocoris borneensis D. A. Polhemus, 1990a: 9. – HT: ♂, Malaysia, Sabah, small forest stream on km 60 on Keningau Highway; USNM.

DISTRIBUTION: **OR:** Malaysia (Sabah, Sarawak!).

Ref.: Chen & Nieser, 1993a; Chen *et al.*, 2005.

Note. First record from Sarawak is based on specimens deposited in the NHMW.

Metrocoris breviculus Chen & Nieser, 1992

Metrocoris breviculus Chen & Nieser, 1992: 156. – HT: ♂, Indonesia, Sulawesi Tengah, SW of Luwuk, between Desa Seseba and Singsing Camp; ZMAN.

DISTRIBUTION. **OR:** Indonesia (Sulawesi Is.).

Ref.: Chen *et al.*, 2005.

Metrocoris cantonensis Chen & Nieser, 1993

Metrocoris cantonensis Chen & Nieser, 1993a: 37. – HT: ♂, China, Guangdong, Dinghu Shan Nature Reserve; NKUM.

DISTRIBUTION. **AS:** China (Guangdong, Guangxi!, Hunan!).

Ref.: Chen & Andersen, 1993; Chen *et al.*, 1993; Chen, 1994; Aukema & Rieger, 1995; Ye *et al.*, 2016.

Note. First records from Guangxi and Hunan are based on specimens deposited in the NHMW.

Metrocoris celebensis D. A. Polhemus, 1990

Metrocoris celebensis D. A. Polhemus, 1990a: 8. – HT: ♂, Indonesia, Sulawesi Tengah, Lore Lindu National Park, upper Palolo Valley, 10 km SE of Kamarora; BMNH.

DISTRIBUTION. **OR:** Indonesia (Sulawesi Is.).

Ref.: Chen & Nieser, 1992; 1993b; 1996; Chen *et al.*, 2005.

Metrocoris ciliatus Boer, 1965

Metrocoris ciliatus Boer, 1965: 23. – HT: ♂, "Burma" [Myanmar], [Tanintharyi] Dawna Hills, 2,000–3,000 ft; BMNH.

DISTRIBUTION: **AS:** China (Yunnan); **OR:** Myanmar (Tanintharyi), Thailand (Chiang Mai), Vietnam (Lai Châu).

Ref.: Chen & Nieser, 1993b; Chen & Zettel, 1998; Cheng *et al.*, 2006; Hutacharern *et al.* 2007; Zettel, 2011a; Aukema *et al.*, 2013; Tran & D. A. Polhemus, 2017.

Note. The female paratypes from Laos designated by Boer (1965) do not belong to this species, but in fact to *M. inthanon* (Chen & Nieser, 1993b: 57).

Metrocoris communis (Distant, 1910)

Euodus communis Distant, 1910a: 151. – HT: nymph, India [Uttarakhand], Kumaon, Sath Tal; BMNH.
Metrocoris stali; Oshanin, 1912: 86 (misidentification; in part, specimens from Iran).
Metrocoris communis (Distant, 1910); Esaki, 1929: 418.
Metrocoris stali; Pradhan, 1950: 102 (misidentification).
Metrocoris omanensis Brown, 1950: 477 (syn. Boer, 1965: 13). – HT: ♂, Oman [United Arab Emirates], Ras-al-Khaima [Ras al-Khaimah]; BMNH.

DISTRIBUTION. **AS:** Afghanistan (Kandahar), Iran (Hormozgan, Kerman, Sistan and Baluchestan, South Khorasan), Iraq (Diyala), Oman!, United Arab Emirates (Fujairah, Ras al-Khaimah, Sharjah); **OR:** India (Chhattisgarh, Haryana, Himachal Pradesh, Karnataka, Kerala!, Madhya Pradesh, Maharashtra, Meghalaya, Odisha, Punjab, Tamil Nadu, Uttarakhand, Uttar Pradesh).

Ref.: Distant, 1910b; China & Miller, 1950; Brown, 1951; Seidenstücker, 1957; Chen & Nieser, 1993b; Linnavuori, 1994; Aukema & Rieger, 1995; Thirumalai, 1999; Thirumalai & Krishnan, 2000; Thirumalai, 2002; 2004; Thirumalai & Sharma, 2005; Thirumalai *et al.*, 2007; Linnavuori *et al.*, 2011; Aukema *et al.*, 2013; Ghahari *et al.*, 2013; Jehamalar & Chandra, 2013a; Basu *et al.*, 2016a.

Notes. Existing records from Oman (e.g. Boer, 1965; Chen & Nieser, 1993b) refer to the United Arab Emirates or India (Linnavuori *et al.*, 2011). However, the presence of *M. communis* in Oman is herein confirmed based on specimens deposited in the NHMW. Additional specimens from the same collection provide basis for the first record from Kerala State, India. The record from Assam State, India, provided by Boer (1965) refers to a locality now part of Meghalaya State, independent from Assam since 1972. The species was listed from the Indian states of Chandigarh and Rajasthan respectively by Thirumalai & Sharma (2005) and Jehamalar & Chandra (2013a), but original records could not be found.

Metrocoris communoides Chen & Nieser, 1993

Metrocoris communoides Chen & Nieser, 1993b: 51. – HT: ♂, India, Shevaroy Hills, Yercaud; SEMC.

DISTRIBUTION. **OR:** India (Kerala, Madhya Pradesh, Tamil Nadu).

Ref.: Thirumalai, 1999; Thirumalai & Krishnan, 2000; Thirumalai, 2002; Thirumalai & Sharma, 2002; Thirumalai *et al.*, 2007; Basu *et al.*, 2016a.

Note. The species was listed from the Indian states of Odisha and Himachal Pradesh by Basu *et al.* (2016a), but the original records could not be found.

Metrocoris compar (White, 1883)

Halobatodes compar White, 1883: 63, 68–69, 78. – LT (Boer, 1965: 17): ♂, "India"; OUM.

Metrocoris compar (White, 1883); Dahl, 1893: 8–9.

DISTRIBUTION: **OR:** Bhutan (Sarpang, Thimphu), India (Arunachal Pradesh, Sikkim, Uttarakhand, West Bengal), Myanmar (Kachin).

Ref.: Lethierry & Severin, 1896; Distant, 1903a; Kirkaldy, 1904; Chen & Nieser, 1993b; Thirumalai, 2002; Bal & Basu, 2003; Zettel & Tran, 2007; Zettel, 2011a; Basu *et al.*, 2016a; Tran & D. A. Polhemus, 2017.

Note. Existing records from Assam, Himachal Pradesh, and Uttar Pradesh (Boer, 1965; Chen & Nieser, 1993b; Thirumalai, 2002; Bal & Basu, 2003; Basu *et al.*, 2016) correspond to localities in other states of northern India mentioned above. Bal & Basu (2003) mistakenly listed the species from Meghalaya State (India), China, Borneo, Java, Sumatra, and Malaysia.

Metrocoris constrictus Chen & Nieser, 1993

Metrocoris constrictus Chen & Nieser, 1993a: 39. – HT: ♂, China, Jiangxi, Lu Shan; NKUM.

DISTRIBUTION. **AS:** China (Jiangxi).

Ref.: Chen & Andersen, 1993; Chen *et al.*, 1993; Chen, 1994; Aukema & Rieger, 1995; Ye *et al.*, 2016.

Metrocoris coxalis Chen & Nieser, 1993

Metrocoris coxalis Chen & Nieser, 1993b: 67. – HT: ♂, "Burma" [Myanmar], Sadon [Sadung], Sheauis Springs; NHRS.

DISTRIBUTION. **OR:** Myanmar (Kachin).

Ref.: Zettel, 2011a.

Metrocoris cylindricus Chen, 1994

Metrocoris cylindricus Chen, 1994: 127. – HT: ♂, China, Hubei, Wufeng County, Hou-he Nature Reserve; NKUM.

DISTRIBUTION. **AS:** China (Hubei).

Ref.: Aukema & Rieger, 1995; Ye *et al.*, 2016.

Metrocoris darjeelingensis Basu, D. A. Polhemus & Subramanian, 2016

Metrocoris darjeelingensis Basu, D. A. Polhemus & Subramanian, 2016a: 269. – HT: ♂, India, West Bengal, Darjeeling District, cascades within Neora Valley National Park; NZSI.

DISTRIBUTION: **OR**: India (Sikkim, West Bengal).

Metrocoris deceptor Basu, D. A. Polhemus & Subramanian, 2016

Metrocoris quynhi; Basu *et al.*, 2015: 98 (misidentification).
Metrocoris deceptor Basu, D. A. Polhemus & Subramanian, 2016a: 267. – HT: ♂, India, West Bengal, Darjeeling District, Rishi River, Rishikhola; NZSI.

DISTRIBUTION: **OR**: India (Himachal Pradesh, Sikkim, West Bengal).

Note. The record from Kerala State, southern India, provided by Bismi & Pilai (2017) is suspicious and needs confirmation.

Metrocoris dembickyi Chen & Zettel, 1999

Metrocoris dembickyi Chen & Zettel, 1999a: 27. – HT: ♂, India, Kerala, 12 km SW of Munnar, Kallar Valley; NHMW.

DISTRIBUTION. **OR:** India (Kerala).

Ref.: Thirumalai, 2002; Basu *et al.*, 2016a.

Metrocoris dentifemoratus Chen & Nieser, 1993

Metrocoris dentifemoratus Chen & Nieser, 1993b: 76. – HT: ♂, China, Hainan, Bawang-lin Nature Reserve; NKUM.

Metrocoris dentiformis; Chen *et al.* 1993: 27 (incorrect subsequent spelling).

DISTRIBUTION. **AS:** China (Hainan).

Ref.: Chen & Andersen, 1993; Chen, 1994; Aukema & Rieger, 1995.

Metrocoris dinendrai Basu, D. A. Polhemus & Subramanian, 2016

Metrocoris dinendrai Basu, D. A. Polhemus & Subramanian, 2016a: 265. – HT: ♂, India, West Bengal, Darjeeling District, roadside cascades within Neora Valley National Park; NZSI.

DISTRIBUTION: **OR**: India (West Bengal).

Metrocoris esakii Chen & Nieser, 1993

Metrocoris lituratus; Esaki, 1926b: 182; Miyamoto, 1961a: 22 (misidentifications).
Metrocoris lituratus; Boer, 1965: 6–8; (misidentification; in part).
Metrocoris esakii Chen & Nieser, 1993a: 39. – HT: ♂, Taiwan, Puli, Nantow Hsien; SEMC.

DISTRIBUTION. **AS:** Japan (Kyushu Is.), Taiwan (Kaohsiung, Nantou, New Taipei, Pingtung, Taipei, Taitung).

Ref.: Chen & Andersen, 1993; Aukema & Rieger, 1995; Azuma *et al.*, 1996; Muraji & Tachikawa, 2000; 2001; Damgaard *et al.*, 2005; BCJ, 2010; ECCIJ, 2016; Ye *et al.*, 2016.

Metrocoris falcatus Chen & Nieser, 1993

Metrocoris sp.?; Matsuda, 1960: 570, fig 793 (specimen from Nepal; see Chen & Nieser, 1993a).
Metrocoris falcatus Chen & Nieser, 1993a: 25. – HT: ♂, India, Uttar Pradesh [Uttarakhand], Dehra Dun Valley; ZMUC.

DISTRIBUTION. **OR:** India (Uttarakhand), Nepal?

Ref.: Thirumalai, 2002; Basu *et al.*, 2016a.

Note. Originally recorded from localities in Uttar Pradesh State (India) that are part of Uttarakhand State since its establishment in November, 2000.

Metrocoris falciformis Ye, Chen & Bu, 2016

Metrocoris falciformis Ye, Chen & Bu, 2016: 369. – HT: ♂, China, Sichuan Prov., Bazhong City, Pingchang County, Zhenlong Mountain Forest Park; NKUM.

DISTRIBUTION. **OR:** China (Sichuan).

Metrocoris femoratus (Paiva, 1919)

Metrocoropsis femorata Paiva, 1919: 365. – HT: ♂, India, Assam [Meghalaya], Garo Hills, stream in dense jungle, above Tura; NZSI.
Metrocoris femorata (Paiva, 1919); Esaki, 1926a: 130.
Metrocoris femoratus (Paiva, 1919); Boer, 1965: 16.

DISTRIBUTION: **OR:** India (Meghalaya).

Ref.: Kemp & China, 1924; Chen & Nieser, 1993a; Thirumalai, 2002; Tran & Zettel, 2005.

Note. Originally recorded from a locality in Assam State (India) that is part of Meghalaya State since its establishment in 1972.

Metrocoris foveatus (Distant, 1910)

Gerastratus foveatus Distant, 1910a: 149. – HT: nymph, India, [Uttarakhand], Kumaon, Bhimtal; BMNH.
Metrocoris foveatus (Distant, 1910); Esaki 1929: 417.

DISTRIBUTION. **OR:** India (Uttarakhand).

Ref.: Distant, 1910b; Boer, 1965.

Note. This taxon is based on a nymph and a *nomen dubium*.

Metrocoris genitalis Chen & Nieser, 1993

Metrocoris genitalis Chen & Nieser, 1993a: 26. – HT: ♂, China, Yunnan, Menglong, Mensong, Xishuangbanna; NKUM.

DISTRIBUTION. **AS:** China (Yunnan); **OR:** Thailand (Chiang Mai).

Ref.: Chen & Andersen, 1993; Chen, 1994; Aukema & Rieger, 1995.

Metrocoris guizhouensis Ye, Chen & Bu, 2016

Metrocoris guizhouensis Ye, Chen & Bu, 2016: 371. – HT: ♂, China, Guizhou Prov., Zunyi City, Suiyang County, Kuankuoshui Nature Reserve; NKUM.

DISTRIBUTION. **OR:** China (Guizhou).

Metrocoris heineri Chen & Zettel, 1999

Metrocoris heineri Chen & Zettel, 1999a: 21. – HT: ♂, China, Hunan, Dayong Distr., Wulingyuan, Zhangjiajie Forest NP, Shuiraosimen; NHMW.

DISTRIBUTION: **AS:** China (Hunan).

Ref.: Aukema *et al.*, 2013; Bai *et al.*, 2014; Ye *et al.*, 2016.

Metrocoris hirtus Chen & Nieser, 1993

Metrocoris hirtus Chen & Nieser, 1993b: 68. – HT: ♂, China, Sichuan, Guan County, Qing-cheng-hou-shan, Tai-an-si; NKUM.

DISTRIBUTION. **AS:** China (Sichuan).

Ref.: Chen & Andersen, 1993; Chen *et al.*, 1993; Chen, 1994; Aukema & Rieger, 1995; Tran & D. A. Polhemus, 2017.

Metrocoris histrio (White, 1883)

Halobatodes histrio White, 1883: 63, 66. – LT (Boer, 1965: 21): ♀, "Japan"; ZMB.
Metrocoris histrio (White, 1883); Dahl, 1893: 8–9.

DISTRIBUTION. **AS:** Japan (Hokkaido Is., Honshu Is., Kyushu Is., Oki Is., Ryukyu Arch., Shikoku Is., Tsushima Is.), North Korea (Kangwon), South Korea (Busan, Daegu, Gyeonggi-do, Gyeongsangbuk-do, Gyeongsangnam-do, Jeollabuk-do, Jeollanam-do, Seoul).

Ref.: Girard, 1885; Witlaczil, 1886; Lethierry & Severin, 1896; Kirkaldy, 1904; Matsumura, 1904; Oshanin, 1908; 1912; Esaki, 1916; 1926a; Matsumura, 1930; 1931; 1932; Esaki, 1932; Hoffmann, 1941; Esaki, 1950; 1955; Miyamoto, 1957; Matsuda, 1960; Miyamoto, 1961a; 1961b; 1962; Miyamoto & Lee, 1963; Hiura, 1967; Josifov & Kerzhner, 1972; Sakamoto & Nakasu, 1972; Kimata, 1990; Koga & Hayashi, 1993; Chen & Nieser, 1993b; Lee & Kwon, 1994; Aukema & Rieger, 1995; Kwon *et al.*, 1996; Kishimoto *et al.*, 1998; Muraji & Tachikawa, 2000; Kwon *et al.*, 2001; Nakatani, 2001; Suzaki, 2002; Hayashi & Ozaki, 2004; Damgaard *et al.*, 2005; Enju, 2007; Pérez-Goodwyn & Fujisaki, 2007; Fukushima *et al.*, 2007; Tsutsumi *et al.*, 2008; Hayashi, 2008; Pérez-Goodwyn *et al.*, 2009; Tokuyama *et al.*, 2009; Lee *et al.*, 2009; Yazaki, 2009; Kuratani *et al.*, 2010; BCJ, 2010; Park *et al.*, 2010; Jung *et al.*, 2011; Sarashina *et al.*, 2011; Iwasaki & Yamada, 2011; 2012; Yano *et al.*, 2012; Lee *et al.*, 2013; Kanai *et al.*, 2014; Yasuda, 2014; Sekimoto *et al.*, 2014; Umamoto *et al.*, 2015; ECCIJ, 2016.

Note. Considering the known distribution of the species and the absence of other reports from China, the record from Zhejiang Province provided by Chen *et al.* (1995) is unreliable.

Metrocoris hubeiensis Chen, 1994

Metrocoris hubeiensis Chen, 1994: 128. – HT: ♂, China, Hubei, Wufeng County, Yuyang Guan Town; NKUM.

DISTRIBUTION. **AS:** China (Hubei).

Ref.: Aukema & Rieger, 1995; Ye *et al.*, 2016.

Metrocoris hungerfordi Boer, 1965

Metrocoris hungerfordi Boer, 1965: 26. – HT: ♂, "Burma" [Myanmar], Shingbwiyang [Shin Bway Yang]; SEMC.

DISTRIBUTION: **OR:** Myanmar (Kachin).

Ref.: Chen & Nieser, 1993b; Zettel, 2011a.

Metrocoris indicus Chen & Nieser, 1993

Metrocoris stali; Distant, 1903a: 190; Boer, 1965: 9 (misidentifications; in part, specimens from southern India).

Metrocoris stali; Annandale, 1919: 118; Matsuda, 1960: 571, fig. 785; Thirumalai, 1989: 46–47; 1994: 37, 40 (misidentifications).

Metrocoris indicus Chen & Nieser, 1993b: 48. – HT: ♂, India, Tamil Nadu, Kodaikanal, Pulney [Palni] Hills; USNM.

DISTRIBUTION. **OR:** India (Karnataka, Kerala, Maharashtra, Tamil Nadu).

Ref.: Thirumalai, 1999; Thirumalai & Krishnan, 2000; Thirumalai, 2002; 2004; Basu *et al.*, 2016a; Bismi & Pillai, 2017.

Metrocoris inthanon Chen & Nieser, 1993

Metrocoris ciliatus; Boer, 1965: 23–26 (in part, female paratypes).
Metrocoris inthanon Chen & Nieser, 1993b: 57. – HT: ♂, Thailand, Chiang Mai, Doi Inthanon National Park, road to summit; ZMUC.

DISTRIBUTION. **OR:** Laos (Champasak, Vientiane, Xiangkhouang), Thailand (Chiang Mai, Mae Hong Son, Phetchabun), Vietnam (Gia Lai, Hà Tĩnh, Lâm Đồng, Nghệ An, Ninh Thuận, Phú Thọ, Quảng Bình, Thanh Hóa).

Ref.: Zettel & Chen, 1996; Chen & Zettel, 1998; Chen *et al.*, 2006b; Hutacharern *et al.* 2007; Tran & D. A. Polhemus, 2017.

Metrocoris johnpolhemi Tran & D. A. Polhemus, 2017

Metrocoris johnpolhemi Tran & D. A. Polhemus, 2017: 119. – HT: ♂, Vietnam, Hanoi, Ba Vi N'Park, stream near Coste 400; ZMHU.

DISTRIBUTION: **OR**: Vietnam (Hà Nội, Lai Châu, Phú Thọ).

Metrocoris lavitra Basu, D. A. Polhemus, Subramanian & Saha, 2016

Metrocoris lavitra Basu, D. A. Polhemus, Subramanian & Saha, 2016a: 261. – HT: ♂, India, West Bengal, Jalpaiguri District, Chapramari Wildlife Sanctuary, stream in front of Chapramari railway gate; NZSI.

DISTRIBUTION: **OR**: India (West Bengal).

Ref.: Tran & D. A. Polhemus, 2017.

Metrocoris lituratus (Stål, 1854)

AQ18 *Halobates lituratus* Stål, 1854: 238. – ST: ♀♂, "China"; NHRS.
Halobatodes lituratus (Stål, 1854); White, 1883: 59, 63–66, 78.
Metrocoris lituratus (Stål, 1854); Dahl, 1893: 8–9.

DISTRIBUTION. **AS:** China (Chongqing, Fujian, Guangdong, Hong Kong, Jiangsu, Jiangxi, Macau, Sichuan, Zhejiang).

Ref.: Dorhn, 1859; Stål, 1860; Mayr, 1866; Frauenfeld, 1867; Walker, 1873; Girard, 1885; Lethierry & Severin, 1896; Kirkaldy, 1901b; 1904; Hoffmann, 1933;

Wu, 1935; Hoffmann, 1941; Matsuda, 1960; Chen & Nieser, 1993a; Chen & Andersen, 1993; Chen *et al.*, 1993; Chen, 1994; Zhang, 1994; Aukema & Rieger, 1995; Chen, 1999; Hua, 2000; Liu & Wang, 2009; Chen *et al.*, 2010; Jiang *et al.* 2011; Ye *et al.*, 2016.

Notes. Existing records from Japan and Sri Lanka (Uhler, 1884; Witlaczil, 1886; Esaki, 1932; Takara, 1957; Miyamoto, 1957; 1961a; Hiura, 1967; Takara & Azuma, 1972; Hua, 2000; Nakatani, 2001) are incorrect. In addition, all those from Taiwan (Esaki, 1925 [as *M. brevis*]; 1926a; 1926c; Hoffmann, 1933; Wu, 1935; Hoffmann, 1941; Miyamoto, 1961a; 1965; 1967; Boer, 1965; Takara & Azuma, 1972; Hua, 2000) probably concern *M. esakii* according to Chen & Nieser (1993a).

Metrocoris luzonicus D. A. Polhemus, 1990

Metrocoris philippinensis; Boer, 1965: 29 (misidentification; in part, female paratype from Manila).
Metrocoris philippinensis Boer, 1965; J. T. Polhemus & Reisen, 1976: 266 (misidentification).
Metrocoris luzonicus D. A. Polhemus, 1990a: 15. – HT: ♂, Philippines, Luzon, Quezon, Quezon National Park, Nalubog Creek; USNM.

DISTRIBUTION. **OR:** Philippines (Luzon Is., Marinduque Is.).

Ref.: Chen & Nieser, 1993b; Chen *et al.*, 2005; Zettel, 2014.

Metrocoris malabaricus Thirumalai, 1986

Metrocoris malabaricus Thirumalai, 1986: 22. – HT: ♂♀, India, Kerala, Silent Valley, AQ19
half way to Valiyaparathodu; NZSI.

DISTRIBUTION: **OR:** India (Karnataka, Kerala, Tamil Nadu).

Ref.: Chen & Nieser, 1993b; Thirumalai, 1999; Thirumalai & Radhakrishnan, 1999; Thirumalai & Krishnan, 2000; Thirumalai, 2002; 2004.

Metrocoris malayensis Chen & Nieser, 1993

Metrocoris strangulator; Cheng & Fernando, 1969: 126; Fernando & Cheng, 1974: 30 (misidentifications).
Metrocoris malayensis Chen & Nieser, 1993a: 15. – HT: ♂, Malaysia, Pahang, Cameron Highlands; ZMUC.

DISTRIBUTION. **OR:** Malaysia (Pahang, Perak).

Ref.: Chen & Zettel, 1998; Cheng *et al.*, 2001; Chen *et al.*, 2005; Tran & D. A. Polhemus, 2017.

Note. Paratypes from Chiang Mai, northern Thailand, were later described as *M. nieseri*.

Metrocoris medius Chen & Nieser, 1996

Metrocoris medius Chen & Nieser, 1996: 72. – HT: ♂, Indonesia, Sulawesi Utara, Pulau Sangihe, Sungai Limu, near Gunung; ZMAN.

DISTRIBUTION. **OR:** Indonesia (Sangihe Is.).

Ref.: Chen *et al.*, 2005.

Metrocoris monticola Tran & D. A. Polhemus, 2017

Metrocoris monticola Tran & D. A. Polhemus, 2017: 135. – HT: ♂, Vietnam, Lao Cai Prov., Sa Pa, Sin Chai, Sin Chai stream, site 1; ZMHU.

DISTRIBUTION: **OR**: Vietnam (Lào Cai).

Metrocoris morsei Jehamalar & Chandra, 2013

Metrocoris morsei Jehamalar & Chandra, 2013b: 64. – HT: ♂, Andaman & Nicobar Islands, Nicobar District, Great Nicobar Biosphere Reserve, Nature Trail; NZSI.

DISTRIBUTION: **OR**: India (Nicobar Is.).

Metrocoris murtiensis Basu, D. A. Polhemus & Subramanian, 2016

Metrocoris murtiensis Basu, D. A. Polhemus & Subramanian, 2016a: 258. – HT: ♂, India, West Bengal, Jalpaiguri District, Gorumara National Park, continuation of Murti River, small pool; NZSI.

DISTRIBUTION: **OR**: India (West Bengal).

Metrocoris nepalensis Distant, 1910

Metrocoris nepalensis Distant, 1910a: 148. – LT (Boer, 1965: 18): ♂, Nepal, Katmandu [Kathmandu]; BMNH.

DISTRIBUTION: **OR:** Bhutan (Punakha, Wangdue Phodrang), India (Uttarakhand), Nepal (Province No. 3).
Ref.: Distant, 1910b; Chen & Nieser, 1993b; Thapa, 2000; Thirumalai, 2002; Zettel & Tran, 2007.

Notes. Recorded from Uttar Pradesh State (India) by Nieser & Chen (1993b) and Thirumalai (2002), but the locality is part of Uttarakhand State since its establishment in November, 2000. Listed from Arunachal Pradesh State by Thirumalai (2002) and Basu *et al.* (2016a), but original record could not be found.

Metrocoris nieseri Chen & Zettel, 1999

Metrocoris nieseri Chen & Zettel, 1999a: 14. – HT: ♂, Thailand, Chiang Mai, Doi Suthep, Hui [Huay] Kaew waterfall; PPCC.

DISTRIBUTION: **OR:** Thailand (Chiang Mai).

Ref.: Hutacharern *et al.* 2007; Kment & Vilínová, 2013; Tran & D. A. Polhemus, 2017.

Metrocoris nigriventris Tran & D. A. Polhemus, 2017

Metrocoris nigriventris Tran & D. A. Polhemus, 2017: 133. – HT: ♂, Vietnam, Lao Cai Prov., Sa Pa, Thanh Phu, near junction of Nam Cang and Muong Hoa streams; ZMHU.

DISTRIBUTION: **OR**: Vietnam (Lai Châu, Lào Cai, Phú Thọ).

Metrocoris nigrofasciatus Distant, 1903

Metrocoris nigrofasciatus Distant, 1903b: 257, pl. 15. – HT: ♂, "Siamese Malay States" [Thailand], [Pattani], "Bulsit Besar" [Bukit Besar]; BMNH.

DISTRIBUTION. **OR:** Malaysia (Kedah, Negeri Sembilan?, Pahang, Penang, Perak, Selangor), Thailand (Nakhon Si Thammarat, Pattani).

Ref.: Distant, 1910b; Matsuda, 1960; Boer, 1965; Cheng & Fernando, 1969; Fernando & Cheng, 1974; D. A. Polhemus, 1990a; Chen & Nieser, 1993a; Zettel, 1993; 1994; Yang & Kovac, 1995; Chen & Zettel, 1998; Cheng *et al.*, 2001; Chen *et al.*, 2005; Hutacharern *et al.* 2007; Tran & D. A. Polhemus, 2017.

Notes. D. A. Polhemus (1990a) indicated that the type locality of *M. nigrofasciatus* would be in Surat Thani Province, Thailand. However, according to the itinerary and map provided by Annandale & Robinson (1903), types were collected in southwestern Pattani Province (see also Clouse & Schwendinger, 2012). He also stated not seeing any true representative of *M. nigrofasciatus* from localities south of Selangor in the Malay Peninsula, which makes records from Negeri Sembilan (Malaysia) questionable. As explained by D. A. Polhemus (1990a) and Chen & Nieser (1993a), records from localities north of the Isthmus of Kra (Distant, 1910b; Paiva, 1918; Kemp & China, 1924; Hafiz & Mathai, 1938; Boer, 1965; Chakrabarty *et al.*, 1993; Lyngdoh, 2010) are incorrect, and those from Johor (Malaysia) and the Indonesian islands of Sumatra and Java (Boer, 1965; Cheng & Fernando, 1969) apply to *M. squamifer*. The record from Langkawi Is. (Malaysia) provided by Boer (1965) may also refer to *M. squamifer*, because this species was recorded from the island by Zettel & Tran (2009), whereas Boer considered *M. squamifer* a synonym of *M. nigrofasciatus*. The record from Sarawak by D. A. Polhemus (1990) is unlikely, as it is far away from the known distribution area; it is probably based on a misidentified specimen of *M. borneensis* – as observed by HZ (unpublished), small macropterous males of *M. borneensis* occasionally lack the species-specific subapical tooth on the forefemur.

Metrocoris nigrofascioides Chen & Nieser, 1993

Metrocoris nigrofascioides Chen & Nieser, 1993a: 34. – HT: ♂, Thailand, Chiang Mai, Horticultural Exp. Stat., 7 km NW of Fang; ZMUC.

DISTRIBUTION. **OR:** Cambodia (Kampong Speu, Koh Kong), Laos (Khammouane, Luang Prabang, Saravane, Vientiane), Malaysia (Langkawi Is., Perak, Tioman Is.), Myanmar (Kachin, Mandalay, Shan), Thailand (Chaiyaphum!, Chiang Mai, Kamphaeng Phet, Kanchanaburi, Khon Kaen!, Mae Hong Son!, Phetchabun!, Phrae!, Sakon Nakhon!, Satun!), Vietnam (Bình Định, Đà Nẵng, Đồng Nai, Gia Lai, Kiên Giang [Phú Quốc Is.], Kon Tum, Lâm Đồng, Phú Yên, Quảng Bình, Thanh Hóa).

Ref.: Yang & Kovac, 1995; Zettel & Chen, 1996; Chen & Zettel, 1998; Yang *et al.*, 1999; Cheng *et al.*, 2001; Hutacharern *et al.* 2007; Lekprayoon *et al.*, 2007; Zettel & Tran, 2009; Zettel, 2011a; D. A. Polhemus & J. T. Polhemus, 2012; Brożek & Zettel, 2014; Tran & D. A. Polhemus, 2017; Zettel *et al.*, 2017; Nowińska & Brożek, 2017.

Notes. The record from Assam State, India, provided by Barman & Gupta (2015) is suspicious and needs confirmation. First records from Thai provinces are based on specimens deposited in the NHMW.

Metrocoris obscurus Chen & Nieser, 1993

Metrocoris obscurus Chen & Nieser, 1993a: 27. – HT: ♂, "Burma" [Myanmar], "Bumgahtaung-Hpungan"; NHRS.

DISTRIBUTION. **AS:** China (Yunnan); **OR:** Myanmar (Kachin), Vietnam (Cao Bằng, Lào Cai).

Ref.: Chen & Andersen, 1993; Chen *et al.*, 1993; Chen, 1994; Aukema & Rieger, 1995; Zettel, 2011a; Tran & D. A. Polhemus, 2017.

Metrocoris pardus Zettel, 2011

Metrocoris pardus Zettel, 2011b: 110. – HT: ♂, Malaysia, West Kelantan, 30 km NW of Gua Musang, Ulu Lalat Mountain, Kampong Sungai Om; NHMW.

DISTRIBUTION: **OR:** Malaysia (Kelantan).

Ref.: Tran & D. A. Polhemus, 2017.

Metrocoris philippinensis Boer, 1965

Metrocoris philippinensis Boer, 1965: 29. – HT: ♂, Philippines, Mindanao, Davao, Mt. Mac Kinley; FMNH.

DISTRIBUTION: **OR:** Philippines (Mindanao Is.).

Ref.: D. A. Polhemus, 1990; Chen & Nieser, 1993b; Chen & Nieser, 1996; D. A. Polhemus, 1998; Chen *et al.*, 2005.

Notes. The female paratype from Manila was later described as *M. luzonicus*. The material of *M. philippinensis* from Los Baños studied by Muraji & Tachikawa (2000) probably also corresponds to *M. luzonicus*. Records by D. A. Polhemus (1990; 1998) from Cebu (Visayas, central Philippines) refer to an undescribed species (HZ, unpublished).

Metrocoris pilosus Chen & Nieser, 1993

Metrocoris pilosus Chen & Nieser, 1993b: 56. – HT: ♂, "Burma" [Myanmar], [Tanintharyi], Dawna Hills; NHRS.

DISTRIBUTION. **OR:** Myanmar (Tanintharyi).

Ref.: Zettel, 2011a.

Metrocoris quynhi Tran & Zettel, 2005

Metrocoris quynhi Tran & Zettel, 2005: 45. – HT: ♂, Vietnam, Lao Cai, Sa Pa, Hoang Lien National Park, upstream of Thac Bac waterfall; ZMHU.

DISTRIBUTION: **OR:** Vietnam (Lai Châu, Lào Cai).

Ref.: Basu *et al.*, 2016a; Tran & D. A. Polhemus, 2017.

Note. Specimens recorded from India by Basu *et al.* (2015) were described as *M. deceptor* by Basu *et al.* (2016).

Metrocoris sapa Tran & D. A. Polhemus, 2017

Metrocoris sapa Tran & D. A. Polhemus, 2017: 137. – HT: ♂, Vietnam, Lao Cai Prov., Sa Pa, Hoang Lien N'Park, Nui Xe, upstream of Suoi Vang; ZMHU.

DISTRIBUTION: **OR**: Vietnam (Lào Cai).

Metrocoris schillhammeri Chen, 1995

Metrocoris schillhammeri Chen, 1995: 156. – HT: ♂, China, Yunnan, 10 km SW of Lijiang; NHMW.

DISTRIBUTION. **AS:** China (Yunnan).

Ref.: Aukema *et al.*, 2013.

Metrocoris shepardi Chen & Zettel, 1999

Metrocoris shepardi Chen & Zettel, 1999a: 19. – HT: ♀, Thailand, Phetchabun [Phitsanulok], Phu Hin Rong Kla NP, Waterwheel Falls; NHMW.

DISTRIBUTION: **OR:** Thailand (Phitsanulok).

Ref.: Chen *et al.*, 2006a; Hutacharern *et al.* 2007.

Note. This species is known only from Phu Hin Rong Kla National Park, which extends through the Thai provinces of Loei, Phetchabun and Phitsanulok. Chen & Zettel (1999a) indicated that the type locality would be in Phetchabun, whereas Chen *et al.* (2006a) treated it as part of Phitsanulok. Coordinates provided by Petersen & Courtney (2010) and Cranston (2016) for the Waterwheel Falls place them in the latter province.

Metrocoris shillongensis Jehamalar & Chandra, 2013

Metrocoris shillongensis Jehamalar & Chandra, 2013b: 66. – HT: ♂, Meghalaya, East Khasi Hills District, Shillong, Botanical Garden; NZSI.

DISTRIBUTION: **OR:** India (Meghalaya).

Ref.: Basu *et al.*, 2016a.

Metrocoris sichuanensis Chen & Nieser, 1993

Metrocoris sichuanensis Chen & Nieser, 1993b: 52. – HT: ♂, China, Sichuan, Guan County, Qingcheng-shan; NKUM.
Metrocoris bui Chen & Zettel, 1999a: 25 (syn. Ye *et al.*, 2016: 360). – HT: ♂, China, Sichuan, Emei Shan, Wanjian Temple; PPCC.

DISTRIBUTION: **AS:** China (Hubei, Sichuan).

Ref.: Chen & Andersen, 1993; Chen *et al.*, 1993; Chen, 1994; Aukema & Rieger, 1995; Aukema *et al.*, 2013; Bai *et al.*, 2014; Tran & D. A. Polhemus, 2017.

Metrocoris sicilis Tran & D. A. Polhemus, 2017

Metrocoris sicilis Tran & D. A. Polhemus, 2017: 131. – HT: ♂, Vietnam, Hanoi, Ba Vi N'Park, stream near Coste 400; ZMHU.

DISTRIBUTION: **OR**: Vietnam (Hà Nội, Phú Thọ).

Metrocoris sinuosus Chen & Nieser, 1993

Metrocoris sinuosus Chen & Nieser, 1993b: 53. – HT: ♂, Sri Lanka, Sabaragamuwa, Kuruwita, Derwood, 6 miles NW of Ratnapura; ZMLU.

DISTRIBUTION. **OR:** Sri Lanka (Sabaragamuwa).

Ref.: Ye *et al.*, 2016.

Metrocoris squamifer Lundblad, 1933

Metrocoris squamifer Lundblad, 1933: 398. – HT: ♀, Indonesia, Sumatra, Ranau; NHRS.

Metrocoris nigrofasciatus; Boer, 1965: 12; Cheng & Fernando, 1969: 125 (misidentifications; specimens from Langkawi Isl.?, Johor, Java, and Sumatra).

DISTRIBUTION. **OR:** Indonesia (Java Is., Sumatra Is.), Malaysia (Johor, Langkawi Is.), Thailand (Phuket).

Ref.: Hungerford & Matsuda, 1960a; Matsuda, 1960; D. A. Polhemus, 1990a; Chen & Nieser, 1993a; Chen & Zettel, 1998; Cheng *et al.*, 2001; Chen *et al.*, 2005; Hutacharern *et al.* 2007; Zettel & Tran, 2009.

Metrocoris stali (Dohrn, 1860)

Halobates stali Dohrn, 1860: 408. – ST: ♂, "Ceylon"; ZMPA. AQ20
Metrocoris brevis Mayr, 1865: 445 (syn. Meinert, 1888: 143). – ST: ♂♂, "Ceylon"; NHMW.
Halobatodes (?) *stali* (Dohrn, 1860); White, 1883: 63, 69–70, 78.
Metrocoris stali (Dohrn, 1860); Meinert, 1888: 143.
Metrocoris illustrarius Distant, 1903a: 189 (syn. Fernando, 1964: 185). – HT: nymph, "Ceylon"; BMNH.

DISTRIBUTION. **OR:** Sri Lanka (Central, Sabaragamuwa, Uva, Western).

Ref.: Mayr, 1866; Dahl, 1893; Lethierry & Severin, 1896; Kirkaldy, 1904; 1906; Esaki, 1926a; Hoffmann, 1941; Matsuda, 1960; Mendis & Fernando, 1962; Boer, 1965; Fernando, 1974; J. T. Polhemus, 1979; Chen & Nieser, 1993b; Ye *et al.*, 2016; Tran & D. A. Polhemus, 2017.

Note. Existing records from China, India, Iran, Japan, and Nepal (Distant, 1903a; Oshanin, 1912; Annandale, 1919; Esaki, 1926a; Hoffmann, 1941; Pradhan, 1950; Mathur, 1953; Hafiz & Pradhan, 1947; Boer, 1965; Thirumalai, 1989; 1994; Bal & Basu, 1994; 2003; B. Chen *et al.*, 2010) are incorrect. The synonymy of *M. illustrarius* is doubtful, because this species is a *nomen dubium* based on a nymph, and two species of *Metrocoris* are known from Sri Lanka: *M. sinuosus* and *M. stali*.

Metrocoris strangulator Breddin, 1905

Metrocoris strangulator Breddin, 1905: 134. – HT: ♂, Indonesia, Java, Tjibodas; ZMUH.

DISTRIBUTION. **OR:** Indonesia (Bali Is.?, Java Is., Sumatra Is.).

Ref.: Bergroth, 1915; Lundblad, 1933; Matsuda, 1960; Boer, 1965; Weidner, 1972; Polhemus, 1990; Chen & Nieser, 1993a.

Notes. Lundblad's (1933) record from Bali was based on two nymphs, which makes it questionable until other specimens are collected on the island. Records from Malaysia and Thailand (Boer 1965; Cheng & Fernando 1969; Fernando & Cheng 1974) are based on misidentifications (D. A. Polhemus 1990a).

Metrocoris stranguloides Chen & Nieser, 1993

Metrocoris stranguloides Chen & Nieser, 1993a: 16. – HT: ♂, China, Hainan, Jian-Feng-Ling Nature Reserve; NKUM.

DISTRIBUTION. **AS:** China (Hainan); **OR:** Laos (Luang Namtha), Vietnam (Bình Định, Đà Nẵng, Gia Lai, Kon Tum, Lâm Đồng, Ninh Thuận, Phú Yên, Quảng Bình, Quảng Ngãi).

Ref.: Chen & Andersen, 1993; Chen *et al.*, 1993; Chen, 1994; Aukema & Rieger, 1995; Tran & D. A. Polhemus, 2017.

Metrocoris strictus Chen & Nieser, 1993

Metrocoris strictus Chen & Nieser, 1993a: 21. – HT: ♂, Thailand, Chiang Mai, Doi Inthanon National Park, Siripum; ZMUC.

DISTRIBUTION. **OR:** Thailand (Chiang Mai).

Ref.: Chen & Zettel, 1998; Damgaard, 2008; Hutacharern *et al.* 2007; Damgaard *et al.*, 2014; Tran & D. A. Polhemus, 2017.

Metrocoris sunda D. A. Polhemus, 1990

Metrocoris sunda D. A. Polhemus, 1990a: 6. – HT: ♂, Indonesia, Nusa Tenggara Barat, Sumbawa, Madsewu River, 2 km above Badindi; BMNH.

DISTRIBUTION: **OR:** Indonesia (Flores Is., Sumbawa Is.).

Ref.: Chen & Nieser, 1993b; Chen *et al.*, 2005; Tran & D. A. Polhemus, 2017.

Metrocoris tenuicornis Esaki, 1926

Metrocoris tenuicornis Esaki, 1926a: 125. – LT (Tran & D. A. Polhemus, 2017: 139): ♂, Laos [Vietnam], Annam; HNHM.

DISTRIBUTION. **AS:** China (Guangdong, Hong Kong); **OR:** Brunei (Temburong), Cambodia (Koh Kong), India (Assam, Sikkim, Uttarakhand), Indonesia (Java Is., Kalimantan Timur, Riau Arch., Sumatra Is.), Laos (Luang Prabang, Vientiane), Malaysia (Johor, Kelantan, Negeri Sembilan, Pahang, Perak, Penang, Sabah, Sarawak, Selangor), Myanmar (Mandalay), Philippines (Mindoro Is., Palawan Is.), Singapore, Thailand (Chiang Mai, Kanchanaburi), Vietnam ("Annam", Điện Biên, Đồng Nai, Gia Lai, Hải Dương, Kiên Giang [Phú Quốc Is.], Kon Tum, Lâm Đồng, Quảng Bình, Quảng Ninh, Thanh Hóa).

Ref.: Hoffmann, 1933; Wu, 1935; Hoffmann, 1941; Boer, 1965; Miyamoto, 1967; Cheng & Fernando, 1969; Fernando & Cheng, 1974; D. A. Polhemus, 1990a; Chen & Nieser, 1993b; Chen & Andersen, 1993; Chen *et al.*, 1993; Chen, 1994; Aukema & Rieger, 1995; Zettel & Chen, 1996; Yang *et al.*, 1997; D. A. Polhemus, 1998; Chen & Zettel, 1998; Hua, 2000; Cheng *et al.*, 2001; Thirumalai, 2002; Bal & Basu, 2003;

Chen *et al.*, 2005; Hutacharern *et al.* 2007; Lekprayoon *et al.*, 2007; Freitag & Zettel, 2012; Basu *et al.*, 2016a; Dalal & Gupta, 2016; Tran & D. A. Polhemus, 2017; Zettel *et al.*, 2017.

Notes. Originally described from "Annam, Laos" (doubfull locality; see discussion in Tran & Polhemus 2017), but the type-locality is actually in central Vietnam. Recorded from a locality in Uttar Pradesh State (India) that is part of Uttarakhand State since its establishment in November, 2000. Listed from the Indian states of Arunachal Pradesh and Meghalaya (Thirumalai, 2002; Bal & Basu, 2003; Basu *et al.*, 2016a), but the original records could not be found. Some Indian records may refer to the recently described *M. lavitra.* Tran & D. A. Polhemus (2017) noted that *M. tenuicornis* may contain a set of cryptic sibling species.

Metrocoris tigrinus D. A. Polhemus, 1990

Metrocoris tigrinus D. A. Polhemus, 1990a: 14. – HT: ♂, Malaysia, Sabah, 12 km S of Ranau; USNM.

DISTRIBUTION: **OR:** Indonesia! (Kalimantan Utara), Malaysia (Sabah).

Ref.: Chen & Nieser, 1993b; Chen *et al.*, 2005; Tran & D. A. Polhemus, 2017.

Note. The first record from the Indonesian part of Borneo is based on a specimen deposited in the NHMW.

Metrocoris triangulatus Zettel & Chen, 1996

Metrocoris triangulatus Zettel & Chen, 1996: 177. – HT: ♂, Vietnam, Buon Luoi, 40 km NW of An Khe; NHMW.

DISTRIBUTION. **OR:** Vietnam (Đà Nẵng, Gia Lai, Kon Tum, Thanh Hóa).

Ref.: Tran & D. A. Polhemus, 2017.

Metrocoris variegans Thirumalai, 1986

Metrocoris variegans Thirumalai, 1986: 25. – HT: ♂, India, Kerala, Silent Valley, Kariamalaithodu; NZSI.

DISTRIBUTION: **OR:** India (Karnataka, Kerala).

Ref.: Chen & Nieser, 1993b; Thirumalai & Krishnan, 2000; Thirumalai, 2002; 2004; Basu *et al.*, 2016a.

Metrocoris velamentus Chen & Nieser, 1993

Metrocoris velamentus Chen & Nieser, 1993b: 61. – HT: ♂, India, Tamil Nadu [Kerala], Travancore, Pirmed; BMNH.

DISTRIBUTION. **OR:** India (Kerala, Tamil Nadu).

Ref.: Thirumalai, 1999; Thirumalai & Krishnan, 2000; Thirumalai, 2002; Basu *et al.*, 2016a.

Note. Chen & Nieser (1993b) associated the type-locality "Pirmed, Travancore" with Tamil Nadu State, India. However, Pirmed (= Peermad, Peermade, Peerumedu, Pirmaad, or Pirmedu) is located in Kerala State (see Francis *et al.* 2002 and Thurston 2011). Paratypes from Tinnevelly (= Tirunelveli) and Kadamparai are indeed from Tamil Nadu.

Metrocoris vietnamensis Tran & Zettel, 2005

Metrocoris vietnamensis Tran & Zettel, 2005: 42. – HT: ♂, Da Nang, Ba Na - Nui Chua, Suoi Nai - Thac Cau Vong (Nai Stream and Rainbow Waterfall); ZMHU.

DISTRIBUTION. **OR:** Vietnam (Đà Nẵng).

Ref.: Tran & D. A. Polhemus, 2017.

Metrocoris xiei Chen, 1994

Metrocoris xiei Chen, 1994: 129. – HT: ♂, China, Guangdong, Ryuang, Babao Shan Nature Reserve; NKUM.

DISTRIBUTION. **AS:** China (Guangdong, Guangzhou!).

Ref.: Aukema & Rieger, 1995; Ye *et al*, 2016.

Note. First record from Guangzhou is based on specimens deposited in the NHMW.

Metrocoris zetteli D. A. Polhemus, 1998

Metrocoris zetteli D. A. Polhemus, 1998: 264. – HT: ♂, Philippines, Mindanao, Misamis Oriental, Mt. Kibungol, 20 km SE of Gingoog; BPBM.

DISTRIBUTION. **OR:** Philippines (Mindanao Is.).

Ref.: Chen *et al.*, 2005.

Metrocoris zhengi Ye, Chen & Bu, 2016

Metrocoris zhengi Ye, Chen & Bu, 2016: 372. – HT: ♂, China, Zunyi city, Daozhen county, Dashahe Nature Reserve, Mopanshi; NKUM.

DISTRIBUTION. **OR:** China (Guizhou).

Genus ***Ventidius*** Distant, 1910 (3 subgenera, 23 species)

Ventidius Distant, 1910a: 149. – Type species by monotypy: *Ventidius aquarius* Distant, 1910.

Subgenus ***Ventidius*** Distant, 1910 (12 species)

Ventidius (*Ventidius*) Distant, 1910a: 149. – Type species by monotypy: *Ventidius aquarius* Distant, 1910.

Ventidius aquarius Distant, 1910

Ventidius aquarius Distant, 1910a: 150. – HT: ♀, India, Travancore, Pallode, 20 miles NE of Trivandrum; BMNH.

DISTRIBUTION. **OR:** India (Karnataka, Kerala, Tamil Nadu), Sri Lanka (Central, Sabaragamuwa, Southern, Uva).

Ref.: Distant, 1910b; Bergroth, 1911; Esaki, 1928b; Hungerford & Matsuda, 1960b; Fernando, 1974; Thirumalai, 1986; Chen & Zettel, 1999b; Thirumalai, 1999; Thirumalai & Radhakrishnan, 1999; Thirumalai & Krishnan, 2000; Thirumalai, 2002; 2004.

Note. Records from Malaysia concern *V. malayensis*.

Ventidius distanti Paiva, 1918

Ventidius distanti Paiva, 1918: 25, pl. VIII, fig. 4. – NT (Chen *et al.*, 2005: 405–406): ♂, Myanmar, Bago Division, Bago Yoma, Sein Ya Forest Camp; NHMW.
Ventidius modulatus Lundblad, 1933: 399 (syn. Chen *et al.*, 2005: 404). – LT (Chen & Zettel, 1999b: 170): ♂, Indonesia, Java (West), Stausee Tjigombong, S of Buitenzorg; NHRS.
Ventidius chinai Hungerford & Matsuda, 1960b: 331 (syn. Chen & Zettel, 1999b: 170). – HT: ♂, "Malay Peninsula", Selangor, Kajang Sungei Lang; BMNH.
Ventidius pubescens Cheng, 1965: 160 (syn. Chen & Zettel, 1999b: 170). – HT: ♂, Malaysia (West), Johor, Muar River at Rompin; BMNH.

DISTRIBUTION. **OR:** Cambodia (Kampong Speu), India, Indonesia (Java Is., Kalimantan Timur, Sumatra Is.), Malaysia (Johor, Kelantan, Malacca, Negeri Sembilan, Pahang, Perak, Selangor, Terengganu, Tioman Is.), Myanmar (Bago, Shan), Singapore, Sri Lanka (Central, Northern, North Western, Sabaragamuwa, Uva), Thailand (Chantaburi, Chiang Mai, Kanchanaburi, Khon Kaen, Lampang, Loei, Maha Sarakham, Phetchabun, Phitsanulok, Songkhla, Surin, Tak, Ubon Ratchathani, Udon Thani), Vietnam (Đồng Nai, Gia Lai, Lâm Đồng, Quảng Trị).

Ref.: Matsuda, 1960; Cobben, 1968; Cheng & Fernando, 1969; Fernando & Cheng, 1974; Fernando, 1974; Yang & Kovac, 1995; Hanboonsong *et al.*, 1996; Zettel & Chen, 1996; Yang *et al.*, 1997; Chen & Zettel, 1998; Yang *et al.*, 1999; Cheng *et al.*, 2001; Thirumalai, 2002; Yang *et al.*, 2004; Lekprayoon *et al.*, 2007; Zettel, 2011a; Suksai *et al.*, 2016; Zettel *et al.*, 2017.

Notes. Listed from the Indian states of West Bengal and Arunachal Pradesh respectively by Chen & Zettel (1999b) and Thirumalai (2002), but original records could not be found. Dover (1928) recorded this species from Malaysia, but his specimens

belong to *V. malayensis* and to an unidentified species of the subgenus *Ventidioides*. Representatives of this unidentified species were mistakenly treated as *V. distanti* by Esaki (1930b).

Ventidius harrisoni Cheng, 1965

Ventidius harrisoni Cheng, 1965: 155. – HT: ♂, Singapore, Seletar River (Sungai Seletar); BMNH.

DISTRIBUTION. **OR:** Indonesia (Kalimantan Timur), Malaysia (Johor, Kelantan, Sarawak, Selangor, Terengganu), Singapore.

Ref.: Cheng & Fernando, 1969; Fernando & Cheng, 1974; Yang *et al.*, 1997; Chen & Zettel, 1999b; Cheng *et al.*, 2001; Chen *et al.*, 2005.

Ventidius henryi Esaki, 1928

Ventidius henryi Esaki, 1928b: 509. – HT: ♂, Sri Lanka, Kitulgala; BMNH.

DISTRIBUTION. **OR:** Sri Lanka (Central, Sabaragabuwa, Southern).

Ref.: Lundblad, 1933; Hungerford & Matsuda, 1960b; Mendis & Fernando, 1962; Matsuda, 1960; Fernando, 1974; J. T. Polhemus, 1979; Chen & Zettel, 1999b.

Ventidius hungerfordi Cheng, 1965

Ventidius hungerfordi Cheng, 1965: 158. – HT: ♂, Malaysia, Selangor, Ampang, Kongsi Lapan River; BMNH.
Ventidius wallacei Lansbury, 1990: 65 (syn. Chen & Zettel, 1999b: 159). – HT: ♂, Malaysia, [Johor, Gunong Ledang], Mt. Ophir; OUM.

DISTRIBUTION. **OR:** Malaysia (Johor, Kedah, Kelantan, Perak, Selangor), Singapore, Thailand (Kanchanaburi).

Ref.: Cheng & Fernando, 1969; Fernando & Cheng, 1974; Yang *et al.*, 1997; Chen & Zettel, 1998; Cheng *et al.*, 2001; Chen *et al.*, 2005; Hutacharern *et al.* 2007; Lekprayoon *et al.*, 2007.

Ventidius longitarsus Chen & Zettel, 1999
Ventidius longitarsus Chen & Zettel, 1999b: 155. – HT: ♂, Vietnam, Da Lak, Mdrak E of Ban Me Thuot; BPBM.

DISTRIBUTION. **OR:** Vietnam (Đắk Lắk, Gia Lai), Laos! (Champasak).

Ref.: Chen & Zettel, 1999.

Note. The first record from Laos is based on specimens deposited in the NHMW.

Ventidius malayensis Hungerford & Matsuda, 1960

Ventidius aquarius; Dover, 1928: 69 (misidentification; part of the specimens from Malaysia); Esaki, 1930b: 18 (misidentification; specimens from Malaysia).

Ventidius malayensis Hungerford & Matsuda, 1960b: 325. – HT: ♂, "Malay Peninsula", Selangor, Sungai Ampang; BMNH.

DISTRIBUTION. **OR:** Brunei (Temburong), Indonesia (Kalimantan Timur, Natuna Is.), Malaysia (Johor, Pahang, Perak, Sabah, Sarawak, Selangor), Singapore, Thailand (Kanchanaburi).

Ref.: Matsuda, 1960; Cheng, 1965; Cheng & Fernando, 1969; Fernando & Cheng, 1974; Chen & Zettel, 1998; Chen & Zettel, 1999b; Cheng *et al.*, 2001; Tran & Yang, 2004; Chen *et al.*, 2005; Hutacharern *et al.* 2007; Lekprayoon *et al.*, 2007; Grinang, 2013.

Ventidius pilosus Chen & Zettel, 1999

Ventidius pilosus Chen & Zettel, 1999b: 169. – HT: ♂, Indonesia, Nusa Tenggara Timur, Sumba, Patawang, 55 km E of Waingapu; JTPC.

DISTRIBUTION. **OR:** Indonesia (Sumba Is., Sumbawa Is.).

Ref.: Chen *et al.*, 2005.

Ventidius polhemorum Chen & Zettel, 1999

Ventidius polhemorum Chen & Zettel, 1999b: 165. – HT: ♂, Malaysia, Borneo, Sabah, 34 km NE of Kota Belud; JTPC.

DISTRIBUTION. **OR:** Malaysia (Sabah, Sarawak).

Ref.: Chen *et al.*, 2005.

Ventidius sushmae Gupta, 1981

Ventidius sushmae Gupta, 1981b: 99. – HT: ♂, India, West Bengal, Darjeeling, Sukna; BSAC.

DISTRIBUTION. **OR:** India (West Bengal).

Ref.: Chen & Zettel, 1999b; Thirumalai, 2002; Basu *et al.*, 2016b.

Ventidius usingeri Hungerford & Matsuda, 1960

Ventidius usingeri Hungerford & Matsuda, 1960b: 326. – HT: ♂, Philippine Islands, Los Baños; FMNH.

DISTRIBUTION. **OR:** Philippines (Luzon Is., Mindanao Is., Polillo Is., Samar Is.).

Ref.: Matsuda, 1960; Chen & Zettel, 1999b; Chen *et al.*, 2005; Damgaard, 2008; Zettel, 2014.

Ventidius werneri Hungerford & Matsuda, 1960

Ventidius werneri Hungerford & Matsuda, 1960b: 330. – HT: ♂, Philippines, Palawan, Puerto Princesa; FMNH.

DISTRIBUTION. **OR:** Philippines (Busuanga Is., Palawan Is.).

Ref.: Matsuda, 1960; Chen & Zettel, 1999b; Chen *et al.*, 2005; Brożek & Zettel, 2014.

Subgenus ***Ventidioides*** Hungerford & Matsuda, 1960 (9 species)

Ventidius (*Ventidioides*) Hungerford & Matsuda, 1960b: 336. – Type species by monotypy: *Ventidius kuiterti* Hungerford & Matsuda, 1960.

Ventidius heissi Chen & Zettel, 1999

Ventidius heissi Chen & Zettel, 1999b: 197. – HT: ♂, Malaysia, Borneo, Sarawak, Kapit District, Merirai Village; BPBM.

DISTRIBUTION. **OR:** Malaysia (Sarawak).

Ref.: Chen *et al.*, 2005.

Ventidius karen Lansbury, 1990

Ventidius karen Lansbury, 1990: 61. – HT: ♂, Thailand, [Nakhon Ratchasima], Khao Yai National Park, Pha Kuai Mai waterfalls; OUM.

DISTRIBUTION. **OR:** Thailand (Nakhon Ratchasima, Phetchabun), Vietnam (Gia Lai).

Ref.: Zettel & Chen, 1996; Chen & Zettel, 1998; 1999b; Chen *et al.*, 2006b; Hutacharern *et al.* 2007.

Ventidius kuiterti Hungerford & Matsuda, 1960

Ventidius kuiterti Hungerford & Matsuda, 1960b: 333. – HT: ♂, "Burma" [Myanmar], Shingbwiyang [Shin Bway Yang]; SEMC.

DISTRIBUTION: **OR:** Myanmar (Kachin).

Ref.: Matsuda, 1960; Chen & Zettel, 1999b; Zettel, 2011a.

Note. The species was mistakenly listed from Arunachal Pradesh (India) by Chen & Zettel (1999b) and Thirumalai (2002), but it is endemic from Myanmar (Zettel, 2011a).

Ventidius kurtokalami Chen & Nieser, 1992

Ventidius kurtokalami Chen & Nieser, 1992: 158. – HT: ♂, Malaysia, Sabah, Danum Valley, 70 km W of Lahad Datu, 4 km S of main trail W5 near Sungai Segama; ZMAN.

DISTRIBUTION. **OR:** Malaysia (Sabah).

Ref.: Chen & Zettel, 1999b; Chen *et al.*, 2005.

Ventidius lundbladi Miyamoto, 1967

Ventidius lundbladi Miyamoto, 1967: 245. – HT: ♂, Thailand, Khao Chong; KUEC.

DISTRIBUTION. **OR:** Thailand (Loei, Nakhon Si Thammarat, Trang).

Ref.: Chen & Zettel, 1998; 1999b; Chen *et al.*, 2005; Hutacharern *et al.* 2007; Suksai *et al.*, 2016.

Ventidius nieseri Chen & Zettel, 1999

Ventidius nieseri Chen & Zettel, 1999b: 196. – HT: ♂, Brunei, Kuala Belalong Field Research [Study] Centre; RMNH.

DISTRIBUTION. **OR:** Brunei (Temburong), Indonesia (Kalimantan Timur), Malaysia (Sarawak).

Ref.: Chen *et al.*, 2005.

Ventidius pulai Cheng, 1965

Ventidius pulai Cheng, 1965: 153. – HT: ♂, Malaysia, Johor, Gunong Pulai; BMNH.

DISTRIBUTION. **AS:** China (Yunnan); **OR:** Laos (Luang Prabang, Xiangkhouang), Malaysia (Johor, Kelantan, Negeri Sembilan, Pahang, Perak, Selangor, Terengganu), Thailand (Chiang Mai, Kanchanaburi, Loei).

Ref.: Cheng & Fernando, 1969; Fernando & Cheng, 1974; Yang & Kovac, 1995; Chen & Zettel, 1998; 1999b; Cheng *et al.*, 2001; Chen *et al.*, 2005; Cheng *et al.*, 2006; Hutacharern *et al.* 2007; Lekprayoon *et al.*, 2007; Aukema *et al.*, 2013.

Ventidius xiphibion Chen & Nieser, 1992

Ventidius xiphibion Chen & Nieser, 1992: 156. – HT: ♂, Indonesia, Sulawesi Tenggara, 8 km E of Sungai Sampara along road Kendari-Wawotobi; RMHN.
Ventidius xiphobion; De Jong, 2004: 39 (incorrect subsequent spelling).

DISTRIBUTION. **OR:** Indonesia (Buton Is., Sulawesi Is.).

Ref.: Chen & Zettel, 1999b; Chen *et al.*, 2005.

Ventidius xyele Chen & Nieser, 1992

Ventidius xyele Chen & Nieser, 1992: 157. – HT: ♂, Indonesia, Sulawesi Utara, R. Toraut, Dumoga Bone National Park; RMHN.

DISTRIBUTION. **OR:** Indonesia (Sulawesi Is.).

Ref.: Chen & Zettel, 1999b; De Jong, 2004; Chen *et al.*, 2005.

Subgenus ***Ventidiopsis*** Miyamoto, 1967 (2 species)

Ventidiopsis Miyamoto, 1967: 247 (as genus). – Type species by original designation and monotypy: *Ventidiopsis imadatei* Miyamoto, 1967.
Ventidius (*Ventidiopsis*) Miyamoto, 1967; Chen & Zettel, 1999b: 199.

Ventidius imadatei (Miyamoto, 1967)

Ventidiopsis imadatei Miyamoto, 1967: 248. – HT: ♀, Brunei, Amo; KUEC.
Ventidius imadatei (Miyamoto, 1967); Chen & Zettel, 1999b: 200.

DISTRIBUTION. **OR:** Brunei (Temburong), Malaysia (Sabah, Sarawak).

Ref.: Chen & Nieser, 1992; Chen *et al.*, 2005.

Ventidius yangae Chen & Zettel, 1999

Ventidius yangae Chen & Zettel, 1999b: 203. – HT: ♀, Indonesia, Sabah, Danum Valley, Palum Tambun; USNM.

DISTRIBUTION. **OR:** Malaysia (Sabah).

Ref. Chen *et al.*, 2005.

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Species groups of Halobatinae

Appendix 2 to: Román-Palacios *et al.* Molecular phylogeny of sea-skaters (*Halobates* Eschscholtz, 1822), relationship between Halobatini and Metrocorini, and catalogue of the subfamily Halobatinae (Hemiptera: Heteroptera: Gerridae).

Genus *Metrocoris* (after Chen & Nieser, 1993a, b; updated)
***Metrocoris anderseni* group:** *M. anderseni*, *M. atlas*, *M. deceptor*, *M. falcatus*, *M. genitalis*, *M. quynhi*
***Metrocoris bilobatus* group:** *M. bilobatoides*, *M. bilobatus*, *M. johnpolhemi*, *M. shepardi*, *M. strictus*, *M. vietnamensis*
***Metrocoris ciliatus* group:** *M. ciliatus*, *M. inthanon*, *M. pilosus*, *M. sicilis*, *M. triangulatus*
***Metrocoris compar* group:** *M. compar*, *M. coxalis*, *M. darjeelingensis*, *M. dinendrai*, *M. hirtus*, *M. monticola*, *M. nepalensis*, *M. nigriventris*, *M. pardus*, *M. sapa*, *M. schillhammeri*
***Metrocoris histrio* group:** *M. histrio*
***Metrocoris lavitra* group:** *M. lavitra*
***Metrocoris lituratus* group:** *M. astictus*, *M. cantonensis*, *M. constrictus*, *M. cylindricus*, *M. esakii*, *M. falciformis*, *M. guizhouensis*, *M. heineri*, *M. hubeiensis*, *M. lituratus*, *M. sichuanensis*, *M. xiei*, *M. zhengi*
***Metrocoris malabaricus* group:** *M. angustus*, *M. dembickyi*, *M. hungerfordi*, *M. malabaricus*, *M. variegans*, *M. velamentus*
***Metrocoris morsei* group:** *M. morsei*
***Metrocoris nigrofasciatus* group:** *M. acutus*, *M. borneensis*, *M. murtiensis*, *M. nigrofasciatus*, *M. nigrofascioides*, *M. squamifer*
***Metrocoris obscurus* group:** *M. obscurus*, *M. shillongensis*
***Metrocoris philippinensis* group:** *M. breviculus*, *M. celebensis*, *M. dentifemoratus*, *M. luzonicus*, *M. medius*, *M. philippinensis*, *M. sunda*, *M. tigrinus*, *M. zetteli*
***Metrocoris stali* group:** *M. communis*, *M. communoides*, *M. indicus*, *M. sinuosus*, *M. stali*
***Metrocoris strangulator* group:** *M. armatus*, *M. femoratus*, *M. malayensis*, *M. nieseri*, *M. strangulator*, *M. stranguloides*
***Metrocoris tenuicornis* group:** *M. tenuicornis*
Nomen dubium: *Metrocoris foveatus* (nymph)

Genus *Ventidius* (after Chen & Zettel, 1999)
***Ventidius* (*Ventidius*) *aquarius* group:** *V. aquarius*, *V. harrisoni*, *V. longitarsus*, *V. malayensis*, *V. usingeri*
***Ventidius* (*Ventidius*) *modulatus* group:** *V. distanti* (= *V. modulatus*), *V. henryi*, *V. hungerfordi*, *V. pilosus*, *V. polhemorum*, *V. sushmae*, *V. werneri*
***Ventidius* (*Ventidioides*) *kuiterti* group:** *V. karen*, *V. kuiterti*, *V. lundbladi*, *V. pulai*
***Ventidius* (*Ventidioides*) *xiphibion* group:** *V. heissi*, *V. kurtokalami*, *V. nieseri*, *V. xiphibion*, *V. xyele*
***Ventidius* (*Ventidiopsis*) *imadatei* group:** *V. imadatei*, *V. yangae*

Genus *Halobates* (after Cheng, 2008; updated)
***H. alluaudi* group:** *H. alluaudi*, *H. tethys*
***H. bryani* group:** *H. bryani*
***H. hayanus* group:** *H. calyptus*, *H. formidabilis*, *H. hayanus*, *H. trynae*
***H. japonicus* group:** *H. galatea*, *H. japonicus*
***H. mariannarum* group:** *H. fijiensis*, *H. katherinae*, *H. kelleni*, *H. mariannarum*, *H. salotae*
***H. masumurai* group:** *H. browni*, *H. elephanta*, *H. esakii*, *H. matsumurai*, *H. nereis*
***H. micans* group:** *H. flaviventris*, *H. hawaiiensis*, *H. micans*, *H. sobrinus*, *H. splendens*
***H. panope* group:** *H. panope*
***H. poseidon* group:** *H. melleus*, *H. poseidon*
***H. princeps* group:** *H. princeps*
***H. proavus* group:** *H. maculatus*, *H. proavus*
***H. regalis* group:** *H. acherontis*, *H. darwini*, *H. dianae*, *H. herringi*, *H. liaoi, H. murphyi*, *H. peronis*, *H. regalis*, *H. sexualis*, *H. whiteleggei*
***H. rivularis* group:** *Halobates rivularis*
***H. robustus* group:** *H. robustus*
***H. sericeus* group:** *H. germanus*, *H. sericeus*
***H. zephyrus* group:** *H. zephyrus*
***H. mjobergi* group:** *H. lannae, H. mjobergi, H. robinsoni,*
Unknown affinity: *H. ruffoi*†

Author Queries:

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