



Towards the conservation of Borneo's freshwater mussels: rediscovery of the endemic *Ctenodesma borneensis* and first record of the non-native *Sinanodonta lauta*

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Abstract

The freshwater mussel fauna of Borneo is highly endemic, with at least 11 species being unique to that island. Most of these species have not been recorded for at least 50 years owing to a lack of sampling effort and large-scale habitat destruction and degradation. Surveys conducted in 2016 across much of Malaysian Borneo failed to locate four out of five native species historically recorded in the study area. The present study aimed to determine the diversity and distribution of freshwater mussels of Brunei and adjacent Limbang Division, Malaysia. In 2018, we conducted interviews with locals, recorded environmental data and surveyed mussels at 43 sites, and conducted interviews at a further 38 sites. Only one population of native mussels, i.e. *Ctenodesma borneensis*, was found in a small tributary of the Limbang River situated in a patch of intact rainforest, representing the first record of this Bornean endemic genus since 1962. In addition, *Sinanodonta lauta* was found in a pond in Lawas district, representing the first record of this species outside its native East Asian distribution. Our data suggest that *C. borneensis* can sustain populations in relatively undisturbed habitats and is likely to have suffered population losses across northern Borneo. The first molecular phylogenetic analysis (COI + 28S) including an endemic Bornean freshwater mussel genus revealed that *Ctenodesma* is phylogenetically divergent from all other previously sampled lineages, rendering it a particularly valuable conservation target.

Keywords Endemic species · Freshwater biodiversity · Non-native species · Threatened species · Tropics · Unionida

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Introduction

Freshwater mussels (Unionida) are one of the most threatened animal groups, with 45% of assessed species being listed as near-threatened, threatened or extinct in the IUCN Red List (IUCN 2019). Causes for the steep declines in diversity and abundance of these filter-feeders, which inhabit the bottom of freshwater habitats across the globe, include direct habitat loss and degradation due to flow modification and pollution, as well as indirect pressures on the catchment, such as increased sedimentation following deforestation (Dudgeon et al. 2006; Lopes-Lima et al. 2018). As mussels fulfil crucial ecosystem services, including water purification, nutrient cycling and food provision, their decline can be detrimental to ecosystems and people, particularly in developing countries (Chowdhury et al. 2016; Vaughn 2018; Zieritz et al. 2018a, 2019). Taxon-based conservation efforts require a sound understanding of the diversity, distribution, ecology and threats to populations, but this information is lacking for most Southeast Asian freshwater mussels (Lopes-Lima et al. 2018; Zieritz et al. 2018b). As a result, the conservation status of 53% of the 135 freshwater mussel species present in Southeast Asia (Zieritz et al. 2018b) has either not been assessed to date or is currently classified as “data deficient” by the IUCN (IUCN 2019).

In regions with high rates of endemism, loss of habitat will lead to particularly high rates of species loss (Myers et al. 2000). The freshwater mussel fauna of Borneo is diverse and highly endemic, with 3–4 of its 10 genera and 11–13 of its 17 species being unique to the island (Table 1; Zieritz et al. 2018b; Graf and Cummings 2019). However, our understanding of the Bornean freshwater mussel assemblage is very limited and most species have not been recorded for several decades (Zieritz and Lopes-Lima 2018). As a result, none of Borneo’s endemic taxa have been included in any molecular phylogenetic context nor have any of them been the subject of any type of conservation assessment (Table 1). Whilst to some extent, this severe lack of knowledge is a result of the lack of targeted surveys, it also may reflect that Bornean freshwater mussels have become more rare and, in some cases, potentially extinct in the course of intense deforestation and habitat destruction since the 1960s (Brook et al. 2003; Iwata et al. 2003; Gaveau et al. 2014). A recent survey across 72 sites and 21 river basins from Sarikei Division in western Sarawak to Kudat Division in eastern Sabah (Fig. 1) failed to locate four out of five native species with historical records from the study area (Zieritz et al. 2018c). Occurrence of the only native species recovered, *Rectidens sumatrensis*, was shown to be strongly negatively associated with the proportion of anthropogenic land cover, and organic and inorganic pollution. In contrast, the non-native invasive species *Sinanodonta* cf. *woodiana* showed positive associations with human influence and is now the most widespread and common freshwater mussel in the study area.

Although a considerable step forward towards understanding northern Borneo’s freshwater mussel diversity, distribution and conservation status, Zieritz et al.’s (2018c) dataset did not include any sites from Brunei or the adjacent Limbang Division of Sarawak. Brunei was identified as an area of particular importance for future surveys because it has retained much of its primary forest (Bryan et al. 2013) and as such, may serve as refuge for Borneo’s endemic mussels. However, records of freshwater mussels from Brunei are confined to a small number of museum lots of the Bornean endemic *Pressidens exanthematicus* with the general location “Brunei” and dating back to before or shortly after the turn of the nineteenth century (i.e. SMF 13878, SMF 13881, UMMZ 110138, UMMZ 110251, USNM 346982; Graf and Cummings 2019). Considering that today’s Limbang

Table 1 Freshwater mussel (Bivalvia: Unionidae) species native to Borneo, including details on their taxonomy, global conservation status, type locality, and distribution across Borneo and globally. Data collated from the mussel-project <https://mussel-project.uwsp.edu/fmuotwaolcb/>; classification follows Pfeiffer et al. (2019) (except *incertae sedis* designation)

Species	Conser- vation status	Type location	Sara- wak	Brunei	Sabah (main- land)	Sabah (Banggi island)	Kali- mantan	Suma- tra	Java	Penin- sular Malaysia	Singa- pore	Thai- land	Viet- nam	Myan- mar	Cam- bodia	Laos
Fam. UNIONIDAE Subfam. Gonideinae Tribe Contradentini																
<i>Contradens</i> <i>contradens</i>	LC	Java					X	X	X	X		X	X	X	X	X
<i>Contradens</i> <i>fulvaste</i> ^a	NL	Kapuas River					X									
<i>Contradens</i> <i>semmelinki</i>	NL	Tanah Laut, South Kalimantan					X	X								
Tribe Rectidentini																
<i>Ctenodesma</i> <i>borneensis</i> ^a	NL	Danau Siriang, Kalimantan	X		X		X									
<i>Ctenodesma</i> <i>schelbeneri</i> ^a	NL	Sungai Batoe, Kampung Moeara Koejian, Unterabt. Sampit, U. Distr. Boven- Sampit" = Central Kalimantan					X									
<i>Hyriopsis</i> <i>velutitzi</i> ^a	NL	Mandai River near Nanga Kalis					X	X								
<i>Rectidens</i> <i>sumatrensis</i>	DD	Danau Luar, Sumatra	X				X	X	X	X	X					

Table 1 continued

Species	Conser- vation status	Type location	Sara- wak	Brunei	Sabah (main- land)	Sabah (Banggi island)	Kali- mantan	Suma- tra	Java	Penin- sular Malaysia	Singa- pore	Thai- land	Viet- nam	Myan- mar	Cam- bodia	Laos
Tribe																
Pseudodontini																
<i>Pseudodon aeneolus</i> ^a	NL	Sebroang and Kapuas Rivers					X									
<i>Pseudodon crassus</i> ^a	NL	Sarawak River	X													
<i>Pseudodon walpolei</i> ^a	NL	Sarawak	X													
Unionidae (incertae sedis)																
<i>Caudicilatus caudiculatus</i> ^a	NL	Danau Siriang, Kalimantan (Pulau Matjan)					X									
<i>Discomya radulosa</i>	NL	Sebroang River					X	X								
<i>Elongaria trompi</i> ^a	NL	Kapuas River, Borneo					X									
<i>Pressidens exanthematicus</i> ^a	NL	East Indies		X												
<i>Pressidens insularis</i>	NL	Banggi island				X										
<i>Schepmania niewenhuisi</i> ^a	NL	Bloc-oe, Ost-Borneo (tributary of Upper Mahakam River)			X		X									
<i>Schepmania parcesculpta</i> ^a	NL	Guléh-Fluss, Ost- Borneo (this river lies near Sangkulirang, East Kalimantan)			X		X									

DD data deficient, LC, least concern, NL not listed, X species confirmed from this region

^aSpecies endemic to Borneo

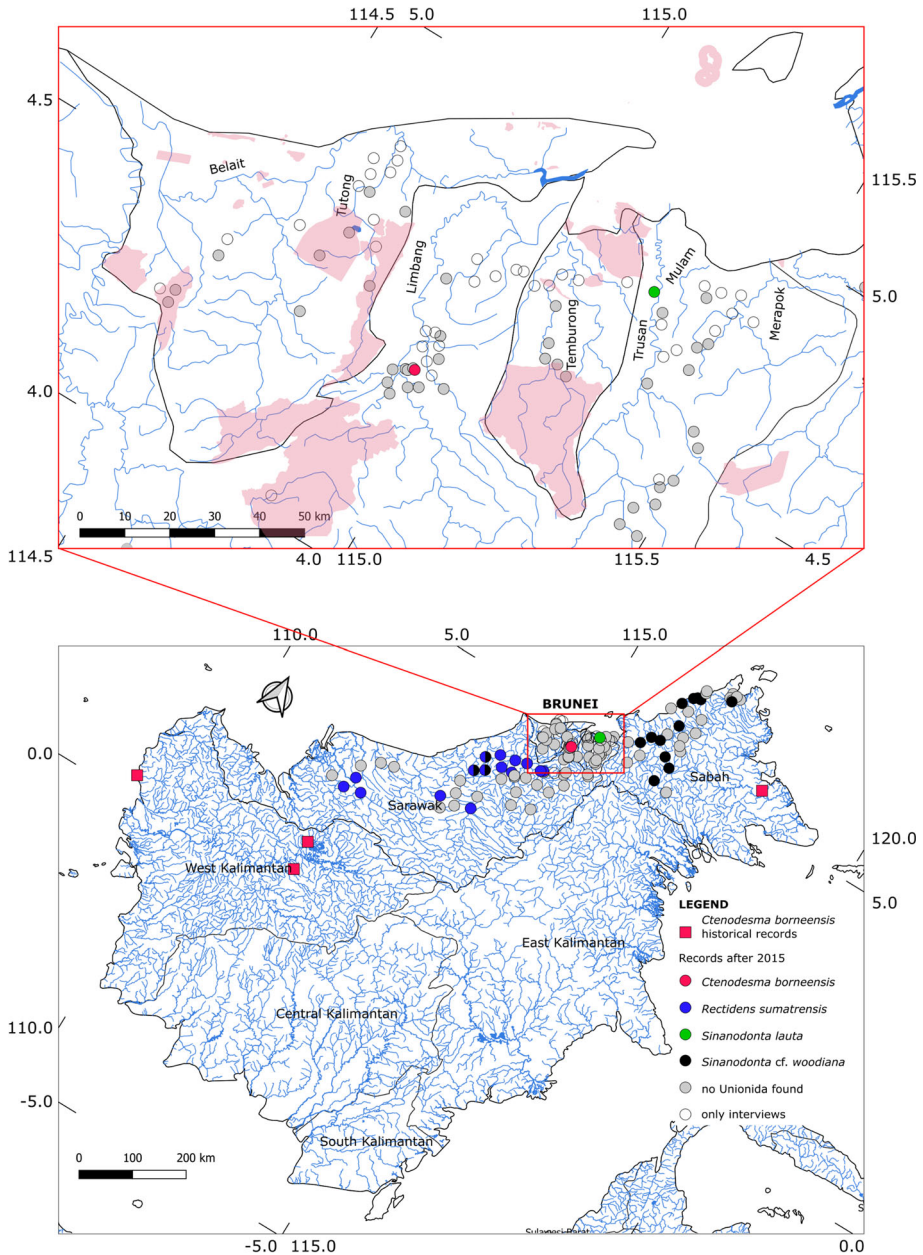


Fig. 1 Location of sites in Borneo surveyed for freshwater mussels (Unionida) from 2015 to 2018 (circles) and of historical records of *Ctenodesma borneensis* (squares). Inset framed in red shows study area and sites surveyed in the course of the present study, with protected areas highlighted in light red

Division, Sarawak, Malaysia, was lost from Brunei to Malaysia in 1890, some or all of these “Brunei” specimens may therefore actually originate from Limbang. In addition, we are aware of two historical records of *R. sumatrensis* from the Limbang River in Limbang

Division (BMNH 39-4-27-57-60, UMMZ 110534), also dating from before or shortly after the turn of the nineteenth century.

The present study aims to determine the diversity and distribution of freshwater mussels in Brunei and Limbang Division through targeted surveys across all the main river basins in the study region. The phylogenetic position of the only Bornean endemic genus sampled (*Ctenodesma*) was then recovered by molecular phylogenetic analysis. Results of this work are subsequently discussed in light of previous work in Malaysian Borneo to draw conclusions on the current state of freshwater mussel biodiversity in northern Borneo.

Methods

Study area

The study area covered about 13,000 km², spanning the Kingdom of Brunei and Limbang Division, Sarawak (Fig. 1). The area is characterised by a tropical rainforest climate and is dominated by shale, siltstone and sandstone deposits, with some limestone in the upper reaches of the Limbang River (Mathew et al. 2016). It is located within the freshwater ecoregion of Northwestern Borneo, which features a diverse and highly endemic fish fauna (Abell et al. 2008; Rahim 2012; Sulaiman et al. 2018). The area includes several protected areas, most notably the National Parks of Tasek Merimbun and Ulu Temburong in Brunei, and Gunung Mulu and Gunung Buda in Limbang Division (Fig. 1).

Field surveys

Field surveys were conducted in the dry season, when water levels are lowest and access to mussels is therefore optimal, in March, April and July 2018. A total of 81 sites were surveyed (inset in Fig. 1), situated in the basins of the Belait, Tutong, Limbang, Temburong, Trusan, Mulam and Merapok rivers (from west to east) (Fig. 1, Online Resource 1). Sites included a range of freshwater habitats, from small, shallow streams (< 1 m width), to large lowland rivers (> 30 m width), as well as standing water bodies such as man-made ponds. Surveys were completed in two stages, i.e. (1) interviews and (2) physical surveys. Access to the site was not deemed safe due to the presence of Estuarine Crocodiles (*Crocodylus porosus*) at 38 sites, which are therefore limited to data from interviews (empty circles in inset of Fig. 1); both interviews and physical surveys were conducted at 43 sites (full circles in inset of Fig. 1).

At each site, covering about 100 m river length, we initially approached local people living or operating in the vicinity of the river (e.g. fishermen) to ask about safe access to the river and the presence of freshwater mussels (see Online Resource 2 for a list of questions put to interviewees). Whenever possible, at least three individuals from diverse demographic groups (age, sex and ethnicity) were interviewed informally at a locality of their choice (usually outside their house or on the river bank) to minimise disruption to them and thus maximise willingness to share their knowledge. Interviewees were thereby shown pictures of the freshwater mussel species previously recorded from northern Borneo. Where access was deemed safe (i.e. absence of crocodiles and river accessible with minimal risk of snake bites or falls), we surveyed for mussels by hand, net and rake following the same protocol as described in Zieritz et al. (2018c). Where mussels were found, voucher specimens and tissue snips were collected and preserved in absolute

ethanol and deposited at the Research Collection of the Universiti Malaysia Sarawak (UNIMAS). Except for vouchers, all other specimens were returned to their habitat.

Measurement of environmental parameters

Several water quality parameters known to affect mussel distribution (see Zieritz et al. 2016; Zieritz et al. 2018c and references therein) were collected at each site: (1) pH, (2) dissolved oxygen (DO), (3) temperature and (4) conductivity were measured in situ using EUTECH pH 5 + (Eutech Instruments Europe BV, Nijkerk, Netherlands), and EXTECH instruments (Extech Instruments Inc., Nahua, NH, USA) SDL150, SDL100 and EC210, respectively. In addition, 300 ml-water samples were collected, of which at least 200 ml were filtered through a Whatman GF/C filter on the evening of the day of collection and 25 ml were immediately processed for analysis of concentrations of (5) total phosphorus (TP) by adding sulfuric acid. GF/C filters were folded, individually wrapped in labelled tin foil and stored together with water samples in the dark on ice whenever possible. Concentrations of (6) soluble reactive phosphorus (SRP) and (7) total ammoniacal nitrogen (TAN) were determined in the laboratory using standard spectrophotometric/colorimetric methods (Lorenzen 1967; Mackereth et al. 1989). (8) Organic matter (OM) concentrations of suspended solids were determined as $(W_{bi} - W_{ai})/V$, where W_{bi} is weight [mg] of GF/C filters and residue after drying at 105 °C for 24 h, W_{ai} is weight [mg] of GF/C filters and residue after 4 h at 550 °C, and V is the volume of water filtered [l]. Concentrations of (9) calcium (Ca^{+}) and (10) potassium (K^{+}) ions were determined through ion chromatography (IC) analysis using a Metrohm Basic 792 ion chromatography system (Metrosep A Supp 4–250 column, with 1 mmol sodium bicarbonate and 3.2 mmol of sodium carbonate eluent at 1.0 ml min⁻¹).

Species identification, and morphological and phylogenetic analysis

Collected specimens were identified to species level through an integrative morphological-molecular approach. DNA was extracted from three specimens of each population using Macherey–Nagel Nucleo-Spin Tissue Kit following the manufacturer's instructions. Cytochrome c oxidase subunit I (COI) mitochondrial DNA was amplified and sequenced in both directions from all extracts using primers and protocol detailed in Zieritz et al. (2016). For native species, we additionally sequenced 28S ribosomal DNA using primers and protocol detailed in Lopes-Lima et al. (2017). Sequences were cleaned up in program MEGA X (Kumar et al. 2018) and deposited on Genbank under Accession Numbers MN900788-900794 and MN902292-902301.

Initial BLAST results of the novel *Ctenodesma* sequences suggested phylogenetic affinities to representatives of the subfamily Gonideinae (sensu Pfeiffer et al. (2019)), especially members of the tribes Rectidentini and Contradentini. We designed our taxon sampling to recover the phylogenetic position of *Ctenodesma* by sampling all representative species of the tribes Rectidentini and Contradentini available on Genbank, as well as representatives of the other tribes of the Gonideinae (Table 2). Molecular matrices were aligned using ClustalW v. 2.1 (Larkin et al. 2007). PartitionFinder2 v 2.1.1 (Lanfear et al. 2017) was used to find the best partition scheme and Generalised time-reversible (GTR) model of nucleotide evolution using the AICc and greedy search algorithm (Lanfear et al. 2012). Maximum-Likelihood (ML) searches were then conducted in IQ-TREE v 1.6.10 (Nguyen et al. 2015) with an initial tree search followed by 10 independent runs and

Table 2 List of sequences from the combined dataset (COI + 28S) used for the phylogenies of the Gonideinae with respective species, countries, voucher numbers, and GenBank references

Species	Code	COI	28S	Voucher	River/Lake	Basin	Country
INGROUP							
<i>Contradens contradens</i>	ConCon1	MF352289	MF352406	RMHB biv211_2	Perak River	Perak	Malaysia
<i>Contradens contradens</i>	ConCon2	DQ191411	AF400692	ANSP 389059	Pahang River	Pahang	Malaysia
<i>Contradens comptus</i>	ConCom_1	MH345973	MH345993	UF 507396 (ICH_471)	Tonle Kong River	Mekong	Cambodia
<i>Contradens comptus</i>	ConCom_2	KX865928	KX865799	RMHB biv119_5	Loei River	Mekong	Thailand
<i>Contradens eximius</i>	ConExi_1	KX865941	KX865812	RMHB biv121_3	Phong River	Mekong	Thailand
<i>Contradens eximius</i>	ConExi_2	KX865936	KX865807	RMHB biv127_1	Chi River	Mekong	Thailand
<i>Contradens misellus</i>	ConMis_1	MH345986	MH346006	UF 507653 (2014_685)	Ping River	Chao Phraya	Thailand
<i>Contradens misellus</i>	ConMis_2	MH345987	MH346007	UF 507653 (2014_687)	Ping River	Chao Phraya	Thailand
<i>Contradens pallegoixi</i>	ConPal_1	MH345988	MH346008	UF 507620 (2014_613)	Pao river	Mekong	Thailand
<i>Contradens pallegoixi</i>	ConPal_2	MH345989	MH346009	UF 507620 (2014_614)	Pao river	Mekong	Thailand
<i>Contradens sp. (Laos)</i>	ConSpL_1	KY561630	KY561662	RMHB biv202_2	Nam Fa River trib	Mekong	Laos
<i>Contradens sp. (Laos)</i>	ConSpL_2	KY561632	KY561664	RMHB biv203_4	Nam Fa River trib	Mekong	Laos
<i>Ctenodesma borneensis</i>	CteBor1	MN900788	MN902292	UNIMAS_X438	Limbang River trib	Limbang	Malaysia
<i>Ctenodesma borneensis</i>	CteBor2	MN900789	MN902293	UNIMAS_X439	Limbang River trib	Limbang	Malaysia
<i>Ctenodesma borneensis</i>	CteBor3	MN900790	MN902294	UNIMAS_X440	Limbang River trib	Limbang	Malaysia
<i>Ensidents cf. ingallianus</i>	EnsIng	KX822641	KX822598	NCSM 84889	Bang Fai River	Mekong	Laos
<i>Ensidents sagittarius</i>	EnsSag1	KP795033	KP795015	UNMZ 304651		Mekong	Cambodia
<i>Ensidents aff.sagittarius</i> sp.2	EnsSag2_1	KX865942	KX865813	RMHB 117_1	Pond near Ban Nong-Bua	Mekong	Thailand
<i>Ensidents aff.sagittarius</i> sp.2	EnsSag2_2	KX865944	KX865815	RMHB 117_3	Pond near Ban Nong-Bua	Mekong	Thailand
<i>Ensidents aff.sagittarius</i> sp.3	EnsSag3_1	KX865948	KX865819	RMHB 123_1	Chi River	Mekong	Thailand
<i>Ensidents aff.sagittarius</i> sp.3	EnsSag3_2	KX865947	KX865818	RMHB 128_3	Chi River	Mekong	Thailand
<i>Ensidents sp.</i>	EnsSp	KX822642	KX822599	NCSM 84902		Mekong	Laos
<i>Hyriopsis bialata</i>	HyrBia	KX051273	MN902295		Pahang River	Pahang	Malaysia
<i>Hyriopsis desowitzi</i>	HyrDes	KX822644	KX822601		Pasak River	Chao Phraya	Thailand

Table 2 continued

Species	Code	COI	28S	Voucher	River/Lake	Basin	Country
<i>Hyriopsis gracilis</i>	HyrGra_1	KX865951	KX865822	RMBH 130_1	Chi River	Mekong	Thailand
<i>Hyriopsis gracilis</i>	HyrGra_2	KX865953	KX865824	RMBH 130_3	Chi River	Mekong	Thailand
<i>Hyriopsis myersiana</i>	HyrMye	KX822645	KX822602		Mae Klong	Mae Klong	Thailand
<i>Hyriopsis</i> sp.	HyrSp	KX383948	MN902296	839512HbB		Chao Phraya	Thailand
<i>Physunio modelli</i>	PhyMod_1	KX865888	KX865759	RMBH biv 131	Chi River	Mekong	Thailand
<i>Physunio modelli</i>	PhyMod_2	KX865883	KX865754	RMBH biv 125_2	Chi River	Mekong	Thailand
<i>Physunio superbus</i>	PhySup	MN900794	MN902297	PhySup_F	Pahang	Pahang	Malaysia
<i>Rectidens sumatrensis</i>	RecSum_1	KX822664	KX822620		Perak	Perak	Malaysia
<i>Rectidens sumatrensis</i>	RecSum_2	MG591508	MN902298	UNIMAS_X314	Sungai Tatan	Baram	Malaysia
<i>Rectidens sumatrensis</i>	RecSum_3	MG591503	MN902299	UNIMAS_X369	Sungai Linau	Suai	Malaysia
<i>Rectidens sumatrensis</i>	RecSum_4	MG591500	MN902300	UNIMAS_X396	Sungai Lalut Pelasan	Batang Kemena	Malaysia
<i>Rectidens sumatrensis</i>	RecSum_5	MG591499	MN902301	UNIMAS_BIV3027	Sungai Sekerubong	Rajang	Malaysia
<i>Trapezoides foliaceus</i>	TraFol_1	MH345979	MH345999	UF 507697 (2012_443)	Pracham Mai River	Mae Klong	Thailand
<i>Trapezoides foliaceus</i>	TraFol_2	MH345983	MH346003	UF 507865 (ICH_2059)	Pracham Mai River trib	Mae Klong	Thailand
<i>Yaukthwa cf. dalliana</i>	YauDal_2	KX865889	KX865760	111_2	Nanyinhka Chaung River	Ayeyarwady	Myanmar
<i>Yaukthwa cf. dalliana</i>	YauDal_1	KX865898	KX865767	103_19	Mansakun River	Ayeyarwady	Myanmar
<i>Yaukthwa inlenensis</i>	YauInle_1	KX865915	KX865786	114_1	Inle Lake Channel	Salween	Myanmar
<i>Yaukthwa inlenensis</i>	YauInle_2	KX865924	KX865795	biv_139_18	Mway Stream	Salween	Myanmar
<i>Yaukthwa nesemannii</i>	YauNes_1	KX865906	KX865777	biv_144_14	Thauk Ye Kupt River	Sittoung	Myanmar
<i>Yaukthwa nesemannii</i>	YauNes_2	MF352256	MF352381	biv_255_4	Thauk Ye Kupt River	Sittoung	Myanmar
<i>Yaukthwa patensis</i>	YauPai_1	MH345970	MH345991	UF 505164 (ICH_638)	Khong River	Salween	Thailand
<i>Yaukthwa patensis</i>	YauPai_2	MH345971	MH345992	UF 507709 (ICH_639)	Khong River	Salween	Thailand
<i>Yaukthwa panhai</i>	YauPan_1	KX865910	KX865781	biv_138_7	Kyan Hone River	Salween	Myanmar
<i>Yaukthwa panhai</i>	YauPan_2	KX865914	KX865785	biv_155_11	Kyan Hone River	Salween	Myanmar
OUTGROUP							

Table 2 continued

Species	Code	COI	28S	Voucher	River/Lake	Basin	Country
<i>Chamberlainia hainesiana</i>	Chamberlainia	KX822635	KX822592				
<i>Lamprotula leaii</i>	Lamprotula	KX822647	KX822604				
<i>Gonidea angulata</i>	Gonidea	KP795030	KP795012	Tissue only	Williamson River	Klamath River	USA
<i>Pseudodon avae</i>	PseAva	KX865858	KX865730	RMBH biv110_5	Lake Indawgyi trib	Sittaung	Myanmar
<i>Pilsbryconcha exilis</i>	PilExi	KP795024	KP795007	UMMZ 304647	Tonle Sap	Mekong	Cambodia

ANSP Academy of Natural Sciences of Philadelphia, NCNM North Carolina Museum of Natural Sciences, UF University of Florida Museum, UMMZ University of Michigan Museum of Zoology, RMBH Russian Museum of the Biodiversity Hotspots, UNIMAS Universiti Malaysia Sarawak

10,000 ultrafast bootstrap replicates using the best codon partitioning scheme and model of nucleotide evolution. Bayesian inference (BI) analysis was performed using MrBayes v 3.2 (Huelsenbeck and Ronquist 2001; Ronquist et al. 2012) using the best codon partitioning scheme and model of nucleotide evolution with 20×10^6 generations sampling every 1000 generations for a total of 20,000 trees with a burnin of 5000. Convergence of the two runs was monitored by the average standard deviation of split frequencies, the potential scale reduction factor (PSRF) and the effective sample size (ESS) of the estimated parameters.

Ctenodesma specimens were analysed for their morphology and anatomy, which included visual examination of shell shape, colour and sculpture, as well as siphons and marsupia under a light microscope. Shell dimensions were measured using sliding calipers to the nearest 0.1 mm.

Results

Diversity and distribution

Out of the 43 sites where both interviews and physical surveys were conducted, only one population of native mussels was found in a tributary of the Limbang River near the village of Kuala Medalam (alternative spelling Mendalam; Fig. 2). The species was identified as *Ctenodesma borneensis* by morphological characters. The species is small and elongated elliptical (Haas 1969), with dimensions of collected specimens being 4.3, 4.8 and 5.0 cm in length, and 2.0, 2.4 and 2.5 cm in height (Fig. 2a). Shells are coloured yellow-greenish to brown with rays and exhibit fine, irregular zig-zag sculpture. Umbos were heavily eroded in all specimens. Inhalant siphons exhibit one row of papillae (Fig. 2b). The one gravid specimen we collected exhibited glochidia in all four demibranchs (tetragenous).

COI and 28S sequences generated for the three specimens were identical (Genbank Accession numbers in Table 2). They were highly divergent from available sequences on Genbank, with the closest match being *Sinoyriopsis cumingii* with 86.3% similarity for COI, and *Hyriopsis* sp., *Ensisens* sp. and *R. sumatrensis* with 97.9–98.1% for 28S.

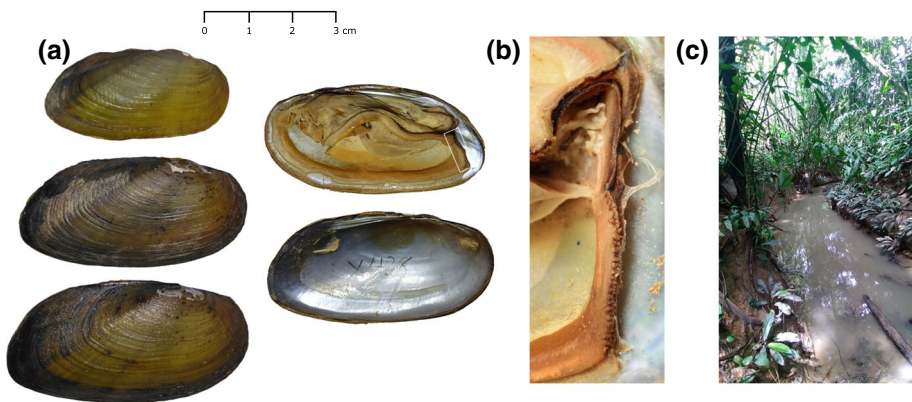


Fig. 2 **a** Exterior and interior view of the three *Ctenodesma borneensis* specimens collected in 2018, **b** detailed picture of siphons (white rectangular area in Fig. 1a), and **c** picture of the sampling site in a tributary of the Limbang River, Sarawak, Malaysia

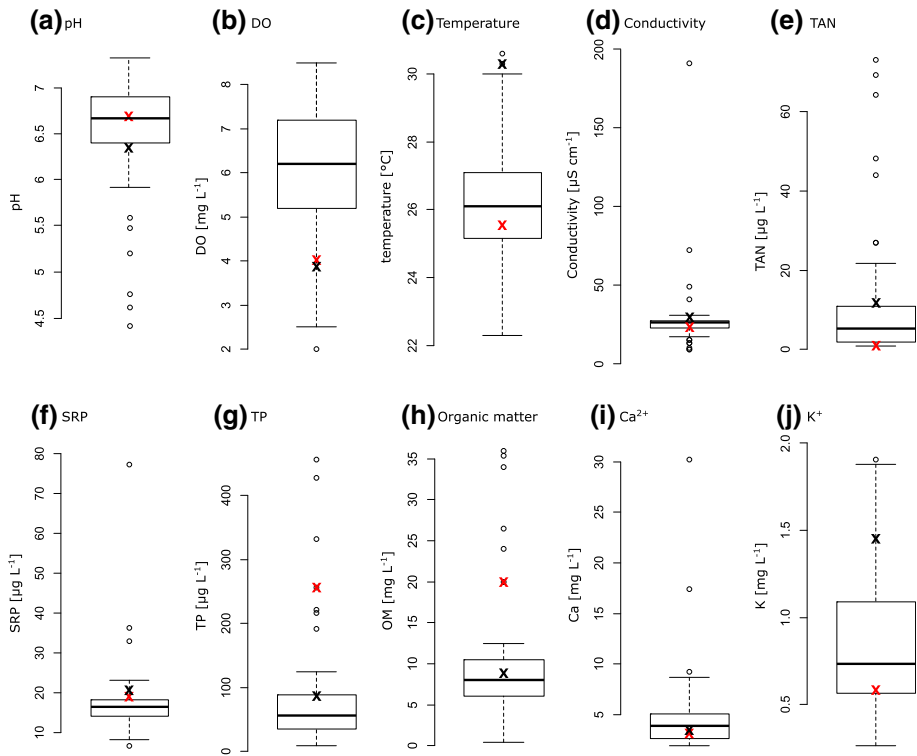


Fig. 3 Variation in water quality parameters across 43 sites in Brunei and Limbang Division, Malaysia (see inset of Fig. 1 for the location of sites). Values at the sites where *Ctenodesma borneensis* and *Sinanodonta lauta* were found are indicated by red and black crosses, respectively

The population was found based on the knowledge and guidance of a local Lun Bawang (an indigenous tribe of this region) and is located in a relatively pristine patch of secondary rainforest only accessible by hiking. The stream was small (< 2 m width) and shallow (< 1 m depth), with a muddy substrate and abundant dead wood and leaf litter material (Fig. 2c), which was also recorded as high TP and OM concentrations in the water (Fig. 3). Other water chemistry parameters indicated good water quality with almost neutral pH, and low conductivity, nutrients and K⁺ concentrations (Fig. 3). Nevertheless, *C. borneensis* population density was low, as only three specimens were found over a 4-person hour survey time.

The only other population of freshwater mussels found in our surveys was that of *Sinanodonta lauta* in a pond in Lawas District, Limbang Division, about 2.5 km east of the border to Brunei (Fig. 1). Being morphologically very similar to the widespread *S. cf. woodiana*, this population was identified through DNA barcoding. COI sequences were generated for three specimens (Genbank Accession Numbers MN900791-93), all of which were identical and matched with Haplotype 54 of *S. lauta* (Lopes-Lima et al. 2020). The specimens had been intentionally introduced to the pond by the owner a few years before, who had bought them from a market in Lawas town. Density was very high and several dozen specimens were sampled within 15 min. Water chemical parameters indicated

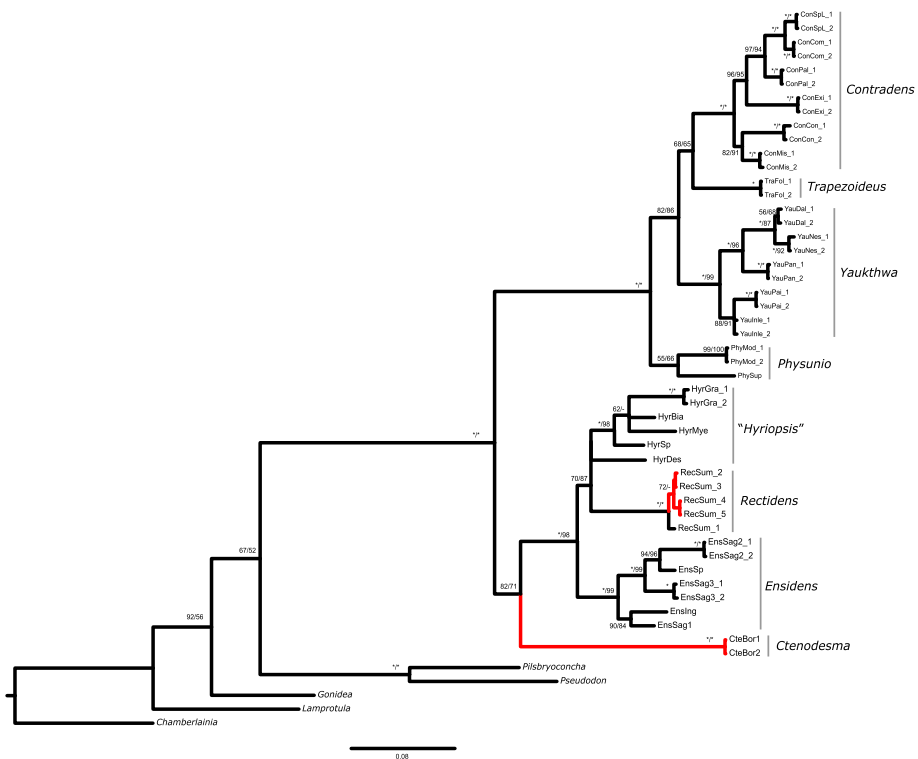


Fig. 4 Bayesian phylogenetic reconstruction (COI + 28S) of the Gonideinae with support values listed as posterior probabilities / ultrafast bootstraps (PP/UF). Values of PP and UF < 50 are marked with “-”; values of PP and UF = 100 are marked with “**”. Red branches indicate lineages sampled from Borneo

slightly elevated TAN and K^+ concentrations, and a water temperature of $> 30^\circ\text{C}$ (Fig. 3).

Interviews at sites that could not be surveyed physically did not reveal any additional potential occurrences of mussels except for one anecdotal record of dense mussel populations in the upper Baram River basin in Gunung Mulu National Park (Fig. 1). Despite interviewing > 100 people at 20 sites across Brunei, there was no indication of the presence of freshwater mussels in Brunei in the past or present.

Phylogenetic position of *Ctenodesma*

The most likely partitioning and modeling scheme was to treat all subsets (28S, COI_pos1, COI_pos2, COI_pos3) as separate partitions using the GTR + G model of nucleotide evolution. Convergence of the BI analysis was supported by the average standard deviation of split frequencies (0.001876), average PRSF values (1.000), and high ESS values (> 3000). The BI and ML reconstructions recovered identical supraspecific relationships except for a minor difference in the sister relationships with *Hyriopsis* (Fig. 4). *Ctenodesma* was recovered as sister to sampled representatives of the tribe Rectidentini

(*Hyriopsis*, *Rectidens* and *Ensidens*), however, this clade had limited support (82 PP/72 UFBS).

Discussion

Rediscovery, population status and phylogeny of *Ctenodesma borneensis*

Our work has resulted in the first confirmation of a population of *C. borneensis* for 57 years. The species was first described in 1874 from Lake (Danau) Seriang (alternative spelling Siriang), Kapuas basin, West Kalimantan, Indonesia, and has a presumed native distribution covering West Kalimantan, Sarawak, and Sabah (Fig. 1; Table 1). To our knowledge, two museum lots exist from “Sarawak”, dated from 1937 and 1945, respectively (Graf and Cummings 2019). The latest record is that by N.S. Haile from 1962 from Gomantong, Sandakan Residency, Sabah, Malaysia.

Although our find is certainly encouraging for freshwater mussel conservation, *C. borneensis* has likely declined in its area of occupancy and is now extremely rare, consisting of only isolated populations in the north and potentially other parts of Borneo. The population presented in this paper remains the only one we found across an area of 150,000 km² and 115 sites that have been surveyed for freshwater mussels from 2016 to 2018 (Zieritz et al. 2018c) (Fig. 1). Furthermore, although several other sites in the immediate proximity of the site where *C. borneensis* was found were surveyed, no further populations could be found (inset of Fig. 1). Finally, the population density of the identified population was extremely low.

The reasons for the apparent decline of this species may be linked to the large-scale deforestation across Borneo. The fact that the only two populations of *C. borneensis* recorded by scientists in the past 60 years inhabit streams within dense rainforests (the second site being Gomantong, which has been a designated Protection Forest Reserve since 1984; UNEP-WCMC and IUCN 2014–2020) suggests that the species may be particularly sensitive to human pressures. The Limbang River is known for its geological complexity, and susceptibility to erosion and flash floods (Krishnan et al. 2017). Ongoing and expanding deforestation activities in this area (World Resources Institute 2014) may therefore pose a particular threat to the integrity of the potential habitats for *C. borneensis* and other freshwater taxa.

Our phylogenetic analyses for the first time include an endemic Bornean freshwater mussel genus, i.e. *Ctenodesma*, which revealed that this genus represents (part of) a highly distinct and previously unsampled molecular phylogenetic lineage (Fig. 4), thereby identifying it as a particularly valuable conservation target (Faith 1996). Specifically, *Ctenodesma* was recovered as the sister-group to the Rectidentini and exhibited morphological characteristics typical of this tribe, including tetragenous marsupia (Lopes-Lima et al. 2017). Of the three Rectidentini genera sequenced to date, *Ensidens* and *Hyriopsis* are distributed across SE-Asia, whilst *Rectidens* is restricted to Sundaland (i.e. Java, Sumatra, Peninsular Malaysia and Borneo) (Graf and Cummings 2019). The non-monophyly of the Borneo samples included in our analysis (*Rectidens* and *Ctenodesma*) suggest multiple lineages have colonised Borneo, and appear to have done so by different mode and tempo. *Rectidens* appears to have more recently and more completely dispersed across Sundaland, whereas *Ctenodesma* appears to represent a relatively older colonisation event. Several other Sundaland endemics have been hypothesised to belong to various clades of the subfamily Gonideinae, including *Caudiculatus* (Chamberlainini), *Elongaria* and

Prohyriopsis (Rectidentini), and *Pressidens* (Contradentini) (Graf and Cummings 2019; Pfeiffer et al. 2019); however, these taxa have yet to be included in a molecular phylogenetic reconstruction. The inclusion of these phylogenetically unsampled lineages will be useful in more completely estimating the evolutionary and biogeographic history of the freshwater mussels of Sundaland. Improved sampling of the Bornean and greater Sundaland fauna will also elucidate whether the recovered long branch of *Ctenodesma* represents a relict and depauperate lineage or a more diverse, but currently undersampled, radiation.

Introduction of non-native freshwater mussels

Whilst native mussels are likely declining in northern Borneo, our study revealed the introduction of a second non-native freshwater mussel species (in addition to *S. cf. woodiana*) to this island, i.e. *S. lauta*. The population from a pond in Limbang Division represents the first record of this species outside its native distribution in Japan, Korea and Southeast Russia (Lopes-Lima et al. 2020). This species is distinct but closely related to *S. cf. woodiana*, native to the Yangtze basin, which is actively spread, repeatedly introduced and very common in Sabah, and is also present in the Suai basin, Sarawak (Zieritz et al. 2018c; Lopes-Lima et al. 2020). The main vectors for ongoing introductions and spread of *Sinanodonta* in Borneo is indirect through fish that are infected with mussel larvae, which live as ectoparasites on fish gills and fins (Wächtler et al. 2001), as well as direct and intentional spread by humans for ornamental purposes and as a food source (Zieritz et al. 2018c). Introductions appear to be usually confined to ponds or other man-made water bodies, where native species are unable to survive and reproduce. As such, the current threat posed by non-native freshwater mussels to the native mussel fauna of Borneo appears to be small when compared to the scale of destruction posed by ongoing logging activities across the island (Miettinen et al. 2011).

Status of northern Borneo's mussels in general

Based on the combined dataset from our previous (Zieritz et al. 2018c) and present work, the current situation of northern Borneo's freshwater mussel fauna is very concerning. As discussed in detail by Zieritz et al. (2018c), historical records indicate the native distribution of five species within the boundaries of the area spanning from the Rajang basin in the west to the upper Sembakung, Kinabatangan and Bengkoka basins to the east, i.e. *C. borneensis*, *P. exanthematicus*, *Pseudodon walpolei*, *R. sumatrensis* and *Schepmania nienwenhuii*. Of these, only *R. sumatrensis* appears to occur in healthy population sizes across several river basins of central Sarawak. Whilst *C. borneensis* has now been confirmed from a single site in the Limbang basin, and *S. nienwenhuii* was relatively recently (i.e. in 2000) collected from Sabah (albeit as dead shells only), *P. exanthematicus* and *P. walpolei* have not been found for at least 50 years. The fact that historical records of these two species are largely confined to the area already surveyed by us indicates that they are very rare or potentially already extinct. Future surveys across Borneo will be needed to revalidate this statement and identify any remaining populations of these endemic Bornean mussel species. Currently available data suggest that endemic Bornean mussels can only sustain populations in relatively pristine habitats. Future surveys targeted towards these species should thus focus on protected areas of northern Borneo, including Labi Hills (Sungai Ingei Conservation) in Brunei Darussalam, Gunung Mulu, Gunung Buda, Pulong Tau, Usun Apau and Lanjak Entimau in Sarawak. Remaining populations of Bornean

endemic mussel species in unprotected areas would benefit from retaining or re-establishing riparian buffer zones, which have been shown to be effective in protecting freshwater ecosystems and biodiversity (Luke et al. 2017a, b). Although legislation guidelines in Sarawak state a buffer zone of 5–50 m along all rivers depending on river width, current implementation rate is poor, as non-compliance with these guidelines has limited to no legal consequences (Ligtermoet et al. 2009; Luke et al. 2019).

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Author contributions AZ developed the study, conducted fieldwork, laboratory work, parts of the analyses and led the writing. KWS conducted molecular analyses. HT and KAR planned and conducted fieldwork, and assisted with morphological analysis. JP and MLL conducted fieldwork and phylogenetic analyses. SM contributed to laboratory analyses. ZS advised on fieldwork planning. All authors contributed to writing.

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