Invertebrate Systematics, 2021, **35**, 394–470 https://doi.org/10.1071/IS20044

Taxonomic revision of a radiation of South-east Asian freshwater mussels (Unionidae: Gonideinae: Contradentini+Rectidentini)

John M. Pfeiffer^{DA,E}, Daniel L. Graf^B, Kevin S. Cummings^C and Lawrence M. Page^D

^ADepartment of Invertebrate Zoology, Smithsonian Institution, National Museum of Natural History, 10th and Constitution Avenue NW, Washington, DC 20560, USA.

^BBiology Department, University of Wisconsin – Stevens Point, 800 Reserve Street, Stevens Point, WI 54481, USA.

^CIllinois Natural History Survey, Prairie Research Institute, University of Illinois, 1816 S. Oak Street,

Champaign, IL 61820, USA.

^DFlorida Museum of Natural History, University of Florida, 1659 Museum Road, Gainesville, FL 32611, USA.

^ECorresponding author. Email: pfeifferj@si.edu

Abstract. The tribes Contradentini and Rectidentini (Unionidae) comprise a diverse clade of freshwater mussels endemic to South-east Asia. Our understanding of the diversity and phylogeny of this radiation has improved dramatically in recent years, but this systematic transformation has not yet benefited from comprehensive museum sampling or phylogenomic methods. A synthetic taxonomic revision of the Contradentini+Rectidentini that leverages these useful and accessible methods is needed. We set out to (1) generate a phylogenomic reconstruction of the supraspecific relationships of the Contradentini+Rectidentini using anchored hybrid enrichment, (2) revise the taxonomy and geographic boundaries of the generic and species-level diversity of the radiation, and (3) identify patterns of freshwater mussel diversity and distribution in this clade and discuss the processes that may have precipitated them. Our phylogenomic reconstruction using over 1600 loci, with a total alignment length of over a half a million nucleotides, recovers a well supported phylogeny of the clade that resolves four independent multispecies radiations endemic to the Mekong drainage. We examined, digitised, and imaged 1837 records from 15 natural history museums that provided the necessary data to document the morphological variation and geographic distributions of the focal taxa. We also analysed 860 COI sequences, 519 of which were generated in this study, to better understand the species boundaries and geographic distributions of the recovered clades. We recognise 54 valid species in the tribes Contradentini and Rectidentini, including 9 described herein as new to science. Out of this revision emerged several interesting biogeographic patterns that appear to have resulted from recent stream capture, historical confluence, and intradrainage barriers to dispersal. We hypothesise that these phenomena shaped the diversity and distribution of the Contradentini +Rectidentini, contributing to the formation of several characteristic freshwater mussel provinces in South-east Asia.

Received 28 May 2020, accepted 23 September 2020, published online 10 May 2021

Introduction

The freshwater mussel fauna of South-east Asia is a phylogenetically diverse assemblage, with native representatives in at least four subfamilies and nine tribes of the Unionidae (Zieritz et al. 2018a; Pfeiffer et al. 2019). The tribes Contradentini and Rectidentini are an exclusively South-east Asian radiation, and they are common and diverse in the region's freshwater communities. Portions of this clade have received considerable molecular systematic attention in recent years, and our appreciation for the phylogeny, distribution, and diversity of this radiation has improved dramatically (Pfeiffer and Graf 2013, 2015; Bolotov et al. 2017a, 2017b, 2018, 2019b, 2020; Konopleva et al. 2017, 2019a, 2019b; Lopes-Lima et al. 2017; Zieritz et al. 2018a,

2018*b*, 2020; Pfeiffer *et al*. 2018*a*, 2019; Jeratthitikul *et al*. 2019; Muanta *et al*. 2019).

The rapid influx of systematic knowledge in this radiation has been prompted, in large part, by many recent successful collecting expeditions in the region and Sanger sequencing of the freshly collected material. To put this rapid progress in perspective, at the start of 2015 there was a single cytochrome 'c' oxidase subunit I (*COI*) sequence available on GenBank for the entirety of this radiation. In this study, we analysed 860 *COI* sequences from 42 Contradentini+Rectidentini species (341 previously published sequences, 519 generated herein). The abundance of these recently collected specimens and their associated molecular data have helped to characterise the genetic and morphological variation of the sampled individuals and delimit the geographic distributions of the recovered clades.

However, this approach has often incompletely leveraged the abundance of museum records available to more completely characterise the systematics, morphological variation, and geographic boundaries of the focal taxa. This is an unfortunate and unnecessary omission especially considering the usefulness of several accessible digital resources designed to facilitate collections-based research (Global Biodiversity Information Facility, see https://www. gbif.org/; Integrated Digitized Biocollections, see https:// www.idigbio.org/; and especially relevant to freshwater mussel biodiversity, the MUSSEL Project Database, see http://mussel-project.uwsp.edu/). Examining the relevant museum records is laborious but it is essential to construct biologically useful classifications, characterise intra- and interspecific variation, determine biogeographic details, and estimate historical baselines for determining conservation status.

Furthermore, the handful of molecular markers applied to reconstructing phylogenies of the Contradentini+Rectidentini (or parts thereof) are well known to recover supraspecific relationships that are unstable or inconsistent with previous topologies based on morphological and phylogenomic data (Graf and Cummings 2006*a*; Pfeiffer *et al.* 2019). Resolving the supraspecific relationships of this radiation are necessary to identifying macroevolutionary patterns and processes, including trait evolution, lineage diversification, and biogeographic history.

We aimed to overcome these shortcomings by taking advantage of the abundance of specimen records in multiple major natural history collections and more broadly sampling the genomes of the focal taxa. Specifically, we (1) generated a phylogenomic reconstruction of the Contradentini+Rectidentini using anchored hybrid enrichment, (2) revised the genus- and species-level taxa by synthesising data from museum records and *COI* sequences, and (3) described patterns of freshwater mussel diversity and distribution in South-east Asia and the processes that may have generated them.

Methods

Biogeographic methods

The geographic distribution of each taxon was determined by examining, digitising, and imaging South-east Asian freshwater mussel records at 15 natural history museums. Institutional abbreviations follow Sabaj (2016), with the number of lots digitised and the date they were integrated into the MUSSEL Project Database given in parentheses: ALMNH, Alabama Museum of Natural History, Tuscaloosa (6 lots; 2011); ANSP, Academy of Natural Sciences at Drexel University, Philadelphia (129 lots; 2011); CAS, California Academy of Sciences, San Francisco (4 lots; 2014); FMNH, Field Museum of Natural History, Chicago (67 lots; 2011); INHS, Illinois Natural History Survey, Champaign (15 lots; 2017); MCZ, Museum of Comparative Zoology, Harvard University, Cambridge (61 lots; 2012); MNHN, Museum National d'Histoire Naturelle, Paris (300 lots; 2012); NCSM, North Carolina Museum of Natural Sciences, Raleigh (30 lots; 2017); NHMUK, Natural History Museum, London (116 lots; 2012); SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfort (415 lots; 2014); SMRL, Applied Malacology Center and Mollusk Museum, Bangkok (46 lots; 2016); UF, Florida Museum of Natural History, Gainesville (296 lots; 2017); UMMZ, University of Michigan Museum of Zoology, Ann Arbor (121 lots; 2011); USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC (217 lots; 2011); ZMB, Museum für Naturkunde, Berlin (4 lots; 2006).

Images of specimens and the associated textual information (e.g. catalogue number, locality, collector, species identification) were converted into a standardised form and incorporated into the MUSSEL Project Database (MUSSELpdb) following methods described in previous papers (Graf and Cummings 2006b, 2009, 2011). Species identifications were reviewed for all records and revised as necessary. Precise collection locations were georeferenced using Google Maps (https://www.google.com/maps), while more vague locations (e.g. water bodies, cities, divisions) were estimated using standardised coordinates in the GEOnet Names Server (see https://geonames.nga.mil/gns/ html/index.html). The voucher number, species identification, geocoordinates, drainage, and ecoregion assignments for all digitised records are in the 'Materials examined' (Table S1 of the Supplementary material). More information about the data model, management, and dissemination of the MUSSEL pdb is available at the MUSSEL Project Web Site (www.musselproject.net/).

Dot distribution maps were produced using ArcMap (ver. 10.2.2, see http://www.esri.com). Digitised records refer to those records that have been fully incorporated into the MUSSELpdb (i.e. specimens and labels imaged, textual information normalised). Barcoded records refer to specimen records for which *COI* sequence and locality data are publicly available on GenBank (see https://www.ncbi.nlm. nih.gov/genbank/). Freshwater ecoregions follow Abell *et al.* (2008), with the exception that the Inle Lake ecoregion, rather than a small, independent ecoregion nested within the larger Lower & Middle Salween ecoregion.

The unweighted pair-group method using arithmetic averages (UPGMA) was used to generate a 50% majority rule consensus dendrogram of ecoregions based on species presence or absence data using the recluster.cons function in the R package 'recluster' (ver. 2.8, see https://cran.r-project. org/web/packages/recluster/index.html; Dapporto 2013). Various metrics of phylogenetic diversity were measured using the R package 'picante' (ver. 1.8, see https://cran.rproject.org/web/packages/picante/index.html; Kembel 2010) including measures of Faith's phylogenetic diversity (pd), mean pairwise diversity (ses.mpd), and mean nearest taxon distance (ses.mntd) for the major drainages in Indochina (i.e. Irrawaddy, Sittaung, Salween, Mae Klong, Chao Phraya, Bang Pakong, Chantaburi, Mekong) and the modern landmasses of Sundaland (i.e. Malay Peninsula, Java, Sumatra, Borneo, Palawan). Phylogenetic diversity among drainages and landmasses was measured using the fraction of unique branch lengths among regions (Unifrac) and visualised using non-metric multidimensional scaling (metaMDS). The resultant dendrogram and multidimensional scaling were used to delimit freshwater mussel provinces, similar to those established for freshwater mussels in the United States (Haag 2010, 2012).

Phylogenetic methods

We selected individuals representing 20 species of the Contradentini+Rectidentini for anchored hybrid enrichment (AHE) using the Unioverse probe set (Pfeiffer et al. 2019). DNA was isolated from mantle tissue using a QIAamp DNA Mini Kit (Qiagen, Inc.) and quantified using PicoGreen. Library preparation, enrichment, and Illumina sequencing were done at RAPiD GENOMICS (Gainesville, FL). Libraries were constructed by shearing DNA to an average length of 300 bp followed by an end-repair reaction and ligation of an adenine residue to the 3'-end of the blunt-end fragments. Barcoded adapters were ligated to the libraries followed by PCR amplification. Libraries were pooled into groups of up to 16 samples and the SureSelectxt Target Enrichment System for Illumina Paired-End Multiplexed Sequencing Library protocol (AgilentTechnologies, Santa Clara, CA, USA) was followed for solution-based target enrichment of the Unioverse probe regions. An Illumina HiSeq 3000 was used to generate 100 bp, paired-end reads. Previously published AHE data were downloaded from GenBank's Short Read Archive (Bioproject PRJNA515912) to include an appropriate outgroup (Lamprotula cornuumlunae) and supplement ingroup taxon sampling.

The AHE reads were processed following the AHE data processing pipeline developed by Breinholt et al. (2018) and are described below (step-by-step instructions and scripts are available at https://github.com/mudlark54/Unioverse). TRIM GALORE! (ver. 0.4.0, see www.bioinformatics.babraham.ac. uk/projects/trim_galore/) was used to remove Illumina data with a minimum read size of <30 nt and Phred quality score <20. Loci were assembled using the iterative bait assembly script (IBA.py) of Breinholt et al. (2018) using the Unioverse reference probe regions as baits and modifying the userach target coverage parameters for the 'blast_command_ nal' and 'blast_lter' commands to 0.60 and 0.50 respectively. The Unioverse reference matrix was added to the AHE assemblies and aligned using MAFFT (ver. 7.294, see https://mafft.cbrc. jp/alignment/software/; Katoh and Standley 2013). Gene orthology was determined using two BLASTn-based python scripts designed to identify loci with single hits to the genome and map their location (i.e. s_hit_checker.py and ortholog_filter.py; Breinholt et al. 2018). If more than one sequence existed for an individual at a particular locus the sequence with the greatest coverage was retained using a custom python script (play_for_keeps.py). To reduce the amount of missing data in our datasets, only loci that had a minimum of 70% taxon occupancy were included. The fulllength reads containing the probe regions with more than 70% taxon occupancy were then trimmed using a minimum column density threshold of 60% and a maximum column entropy of 1.5 (Breinholt et al. 2018 - alignment_DE_trim. py). To remove potentially problematic regions on either side of the probe region we used the filtering procedure described by Breinholt *et al.* (2018) (flank_dropper.py), which removed columns with a nucleotide density of less than 60% and a nucleotide entropy of >1.5. The processed full sequences were then split into three separate loci – the head, the probe region, and the tail (Breinholt *et al.* 2018 – extract_probe_region.py). FASconCAT-G_v1.04.pl (ver. 1.04, see https://github.com/PatrickKueck/FASconCAT-G; Kück and Longo 2014) was used to make the concatenated matrices and partition files.

Maximum likelihood (ML) reconstruction of the concatenated datasets was conducted in IO-TREE (ver. 1.6, see http://www.iqtree.org/; Nguyen et al. 2015) using linked partitioned models (Chernomor et al. 2016), ModelFinder (MFP option: Kalyaanamoorthy et al. 2017), and nodal support measured by 1000 ultrafast bootstraps (UFB) (Hoang et al. 2018). IQ-TREE was also used to determine model use and estimate an unpartitioned ML gene tree (MFP option) for each locus using 1000 UFB replicates for subsequent estimation of a species tree using ASTRAL (ver. 5.6.1, see https://github.com/ smirarab/ASTRAL; Zhang et al. 2018). Bipartitions with <10 UFB were removed using Newick Utilities (Junier and Zdobnov 2010) before species tree estimation as this has been shown to improve species tree accuracy (Zhang et al. 2017). Nodal support and gene tree conflict were measured in the ASTRAL analysis using local posterior probabilities. The proportion of bipartitions shared between the concatenated topology and each gene tree was measured using SortaDate (Smith et al. 2018), and these values were compared to various alignment statistics measured by AMAS (Borowiec 2016).

COI sequences were generated from representatives of the Contradentini+Rectidentini to evaluate intraspecific genetic variation and help identify the geographic boundaries of the species-level clades. Primers for polymerase chain reaction (PCR) and sequencing were COI - dgLCO-1490, GGTCAACAAATCAT AAAGAYATYGG, and dgHCO-2198, TAAACTTCAGGGT GACCAAARAAYCA (Meyer 2003). PCR was performed in 25-µL reactions using the following reagents and volumes: H₂0 (17.75 μ L), 5× MyTaq Reaction Buffer (5 µL; Bioline), primers (0.5 µL), MyTaq Red DNA polymerase (0.25 µL) and DNA template (1 µL). Bidirectional Sanger sequencing was performed at the University of Florida Interdisciplinary Center for Biotechnology Research. Raw chromatograms were assembled into bidirectional consensus sequences and edited using Geneious (ver. 6.1.2, see http://www.geneious.com; Kearse et al. 2012). Novel sequences were combined with previously published COI sequences to generate COI gene trees for all available representatives of the Contradentini and Rectidentini. Codon-partitioned COI gene trees were generated using IQ-TREE with model testing and partitioning scheme determined using the MFP+MERGE option, a perturbation strength of 0.2, 1000 UFB, and a minimum support threshold of 0.5.

Biogeographic results

The MUSSELpdb contained 1837 digitised and imaged records from the tribes Contradentini and Rectidentini. Textual information associated with each of these records is in our 'Material examined' (Table S1) and the images are available on the MUSSEL Project webpage. The MUSSELpdb has digitised records for each of the recognised species of the Contradentini (32 spp.) and Rectidentini (22 spp.) with *Lens contradens* and *Hyriopsis myersiana* having the greatest number of records (375 and 122 respectively) (Fig. 1). Of the 1837 records, 1306 could be assigned to an ecoregion (71%) and 1241 could be georeferenced (67%). The digitised records are distributed across 19 ecoregions (Fig. 2), with the Khorat Plateau (374) and Chao Phraya (330) ecoregions having the greatest number of records (Fig. 3). The

distribution of each species across the major drainages of Indochina and the landmasses of Sundaland are reported in Table 1. Various metrics of biodiversity (species richness, endemism, and phylogenetic diversity) for the major drainages of Indochina and landmasses of Sundaland are reported in Table 2.

The Khorat Plateau is the most species-rich ecoregion (17 spp.), followed by the Chao Phraya (12) (Fig. 4). The Contradentini has its greatest species richness in the Sittaung–Irrawaddy (9) and Khorat Plateau ecoregions (8),



Fig. 1. Taxonomic distribution of the digitised records.



Fig. 2. Digitised and barcoded records of the Contradentini+Rectidentini. Black boundaries are freshwater ecoregions delimited by Abell *et al.* (2008).



Fig. 3. Geographic distribution of digitised records.

followed closely by the Chao Phraya (7), Mae Klong (5), and Lower Lancang (5). The Rectidentini has its greatest diversity in the Khorat Plateau (9), followed by the Chao Phraya (5) and Kapuas (4). Of the 54 species of the Contradentini and Rectidentini, 40 are endemic to a single drainage and 32 species are endemic to a single ecoregion (Fig. 5). The Sittaung–Irrawaddy (9) and Khorat Plateau (8) ecoregions have the greatest number of endemic species (Fig. 6). The UPGMA dendrogram of species presence or absence data per ecoregion and NMDS of phylogenetic diversity per drainage and landmass is largely consistent with recognising six zoogeographic provinces in the South-east Asian Subregion (Fig. 7).

Phylogenetic results

Our final AHE matrices included 29 individuals: Contradentini, 15; Rectidentini, 13; and *Lamprotula cornuumlunae* (Table 3). Of the 811 targeted probe regions, 538 had a taxon occupancy greater than 70%. We were able to include the head and tail regions (i.e. flanking regions) associated with each of 538 probe regions for a total of 1614 loci in our fully concatenated dataset (Table 4). In comparison to the probe regions, the flanking regions (i.e. heads and tails) were longer (P < 0.01), contained a greater proportion of parsimony informative sites (P < 0.01), had less GC content (P < 0.01), and shared a greater proportion of bipartitions with the fully concatenated tree (Fig. 8).

Table 4 describes the summary statistics of our five concatenated datasets. Topologies and support values between the five concatenated ML analyses and the ASTRAL analysis were strongly congruent (Fig. 9). The fully concatenated topology (head+probe+tail) and the ASTRAL topology were identical, except with respect to

the sister group of Ensidens dugasti. Maximum likelihood topologies generated using the less inclusive datasets (head only, probe only, tail only, and flanks only) and the ASTRAL analysis are available in Fig. S1–S5 of the Supplementary material. Despite the head and tail regions having very similar molecular properties (Table 4, Fig. 8), the two regions recovered incongruent topologies with respect to the relationships within Lens (Fig. 9). However, when the head and tail regions were analysed together (i.e. flanks) the topology was identical to the fully concatenated matrix and the ASTRAL analysis (except the sister group to *E. dugasti*). In total, 519 COI sequences were generated in this study and were analysed with 341 previously published COI sequences (Table S2 of the Supplementary material) to generate several more taxonomically and geographically inclusive gene trees and better understand the more fine-scale phylogenetic and biogeographic patterns. Tissue samples of the specimens sequenced for these analyses are all available in the Florida Museum's Genetic Resource Repository to ensure open access and facilitate future research (see https://www.floridamuseum. ufl.edu/grr/).

Taxonomy

Family UNIONIDAE Rafinesque, 1820 Subfamily GONIDEINAE Ortmann, 1916 CONTRADENTINI+RECTIDENTINI

Several recent molecular phylogenetic studies have recovered representatives of the tribes Contradentini and Rectidentini as sister taxa and have referred to that clade as the subfamily Rectidentinae (Pfeiffer and Graf 2015; Lopes-Lima *et al.* 2017; Bolotov *et al.* 2018; Konopleva *et al.* 2019a).

Table 1. Distribution of Contradentini+Rectidentini species across the drainages of Indochina and the landmasses of Sundalan	ıd
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	Indeching						Sundaland						
	Irrawaddy	Sittaung	Salween	Mae Klong	Chao Phraya	Bang Pakong	Chantaburi	Mekong	Malay Peninsula	Sumatra	Java	Borneo	Palawan
Contradentini		_						_					
Lens comptus								×					
Lens contradens			~	~	~	~		~	~	~	~		
Lens contratens			~	~	~	^		~	~	~	^		
Lens eximus Lens inornatus				~	~	~		~					
Lens Inornatus				^	^	^						~	
Lens ugens								~				^	
Lens microntomic								Ŷ					
Lens micropierus								~					
Lens miserius					~			×.					
Lens novoseiovi								~					
Lens pullegoixi								~					
Lens roijoranali								~				~	
Dhummia manini												×	
Physinio modelli								~					
Physunio modelli Dhummia mallunai dua								×					
Physunio pellusciaus								×					
Physunio superbus				×	×	×			×	×	×		
Pressidens exanthematicus												×	×
Solenaia emarginata				×	×								
Trapezoideus foliaceus				×	×								
Trapezoideus lenya									×				
Trapezoideus subviridus						×	×						
Yaukthwa avaensis	×												
Yaukthwa baniensis	×												
Yaukthwa dalliana	×												
Yaukthwa elongatula	×												
Yaukthwa inlenensis			×										
Yaukthwa nesemanni		×											
Yaukthwa paiensis			×										
Yaukthwa panhai		×											
Yaukthwa peguensis	×												
Yaukthwa rectangularis	×												
Yaukthwa zayleymanensis	×												
Rectidentini													
Ctenodesma borneensis												×	
Ctenodesma scheibeneri												×	
Elongaria orientalis											×		
Elongaria trompi												×	
Ensidens dugasti								×					
Ensidens ingallsianus				×	×	×		×	×				
Ensidens jaculus								×					
Ensidens sagittarius								×					
Ensidens spiculus								×					
Ensidens telus						×	×	×					
Hyriopsis bialata								×	×				
Hyriopsis delaportei								×					
Hyriopsis desowitzi					×	×							
Hyriopsis khoratensis								×					
Hyriopsis kratiensis								×					
Hyriopsis myersiana				×	×	×		×					
Hyriopsis phuphaniensis								×					
Hyriopsis sakhonensis								×					
Hyriopsis undescribed					×								
Hyriopsis velthuizeni										×		×	
Prohyriopsis stolata										×			
Rectidens sumatrensis									×	×	×	×	

	Species richness				Endemic species			Phylogenetic diversity	Mean pairwise distance within region		Mean nearest taxon distance within region	
	Total	Contradentini	Rectidentini	Total	Contradentini	Rectidentini	Total		Ζ	P	Ζ	P
Irrawaddy	7	7	0	7	7	0	100	0.28	-2.94	<0.01	-2.35	<0.01
Sittaung	2	2	0	2	2	0	100	0.11	-1.52	0.02	-1.52	0.02
Salween	3	3	0	2	2	0	67	0.29	-2.01	0.02	-2.10	0.01
Mae Klong	7	5	2	0	0	0	0	1.45	-0.32	0.28	0.45	0.71
Chao Phraya	10	6	4	2	1	1	20	1.72	-0.17	0.39	0.22	0.62
Bang Pakong	8	4	4	0	0	0	0	1.59	0.52	0.74	0.36	0.68
Chantaburi	2	1	1	0	0	0	0	0.81	0.95	0.74	0.95	0.72
Mekong	24	11	13	19	10	9	79	2.34	-0.95	0.17	-1.89	0.03
Malay Peninsula	6	3	3	1	1	0	16	1.42	0.57	0.77	0.79	0.81
Sumatra	5	2	3	1	0	1	20	0.90	1.22	0.92	1.24	0.94
Java	4	2	2	1	0	1	25	1.00	0.67	0.78	0.54	0.72
Borneo	8	3	5	5	2	3	63	0.94	1.34	0.96	1.34	0.96
Palawan	1	1	0	0	0	0	0	n.a.	n.a.	n.a.	n.a.	n.a.

Table 2. Diversity measures of drainages of Indochina and landmasses of Sundaland Values in bold are considered phylogenetically clustered (<0.05) or phylogenetically even (>0.95)



Fig. 4. Species richness per ecoregion.

However, recent phylogenomic reconstructions have shown that the Rectidentinae is deeply nested within the Gonideinae, rendering the latter subfamily paraphyletic (Pfeiffer *et al.* 2019). We are not philosophically opposed to recognising paraphyletic taxa but only if doing so communicates something useful about the evolutionary history of the paraphyletic clade. Given the uncertainty surrounding the phylogenetic relationships of the tribes of the Gonideinae (Pfeiffer *et al.* 2019) and the lack of synapomorphies uniting the higher-level taxa (Lopes-Lima *et al.* 2017), we see little justification, besides 'branchyness', for recognising a subfamily Rectidentinae nested within a paraphyletic subfamily Gonideinae.

Among this radiation we recognise 54 species, 9 of which are described herein (http://zoobank.org/urn:lsid:zoobank.org:pub:D37EE4AF-C761-403E-BE76-00D0B91E5B33). We



Fig. 5. Histogram of (A) species-drainage occurrence and (B) species-ecoregion occurrence.

included 28 Contradentini+Rectidentini species in our phylogenomic analyses (Fig. 9) and 43 species in our *COI* gene trees. The 11 species from which we were unable to obtain sequence data are restricted to either the Malay Archipelago (8) or the drainages west of the Salween (3). Within the Contradentini+Rectidentini we observed four independent multispecies radiations endemic to the Mekong drainage – each of which is concentrated in the Khorat Plateau ecoregion (Fig. 9). These four multispecies Mekong radiations are distributed across the phylogeny of the Contradentini (*Lens* and *Physunio*) and Rectidentini (*Ensidens* and *Hyriopsis*) and share several molecular, morphological and biogeographic patterns, suggesting that common processes shaped the evolution of these clades.

CONTRADENTINI Modell, 1942

Type: Contradens Haas, 1911.

Diagnosis

Bilaterally asymmetrical glochidia is a clear synapomorphy of the Contradentini and distinguishes that clade from all other freshwater mussels (Pfeiffer and Graf 2015). Morphologically, the Contradentini most closely resembles its sister tribe, the Rectidentini. In comparison to the Rectidentini, which are more elongate and have a more bluntly pointed posterior end, the Contradentini are more circular or rectangular and have a broadly rounded or square posterior end (Fig. 10). The Contradentini also have a more rounded posterior ridge and longer posterior slope,



Fig. 6. Number of endemic species per ecoregion.

whereas the Rectidentini tend to have a sharper posterior ridge and a shorter posterior slope (excluding the wing of *Hyriopsis*). The Contradentini may also be characterised by its generally smooth and shiny, yellow to brown periostracum, often with green rays on the posterior slope (although considerable variation exists among these traits). These green rays typically take the form of two or three green lines corresponding to oblique ridges on the slope. This green pattern on the posterior slope also occurs in other lineages in South-east Asia (e.g. Rectidentini and Indochinellini), but are generally less defined in comparison to the Contradentini. Several taxa also have wrinkles on the posterior slope that run more or less perpendicular to the dorsal shell margin (e.g. *Lens, Yaukthwa*).

Distribution

Widespread in Indochina from the Irrawaddy drainage in the west to the Mekong drainage in the east. Also occurs on the Malay Peninsula and the islands of Sumatra, Java, Borneo, and Palawan.

Genera

We recognise six genera in the Contradentini. Several of these genera are morphologically quite similar and there are few known characters capable of clearly diagnosing them. The lack of known diagnostic characters for these genera is an unfortunate and all too common shortcoming in freshwater mussel systematics. Nevertheless, these names are useful in that they communicate the monophyly of a collection of species.

- Lens Simpson, 1900.
- Physunio Simpson, 1900.
- Pressidens Haas, 1910.

- Solenaia Conrad, 1869.
- Trapezoideus Simpson, 1900.
- *Yaukthwa* Konopleva, Pfeiffer, Vikhrev, Kondakov, Gofarov, Aksenova, Lunn, Chan & Bolotov, 2019.

Remarks

The position of *Pressidens* among the Contradentini remains untested. The umbo sculpture of *Pressidens* is quite unusual for the Contradentini but this genus shares several other similarities with the clade including shell outline, dentition, and periostracum colour and texture.

Key to the genera of the Contradentini

The practicality of this key is complicated by considerable intrageneric and intraspecific variation, but it may serve as a useful starting point.

- 1. Rectangular, subrectangular shell outline
 2

 Circular, ovate, rhomboidal, trapezoidal shell outline
 3
- Ultra-elongate, posterior end >2× taller than anteriorSolenaia Elongate, posterior end <2× taller than anteriorYaukthwa

Genus Lens Simpson, 1900 stat. rev.

- Lens Simpson, 1900: 831. Type species: Unio eximius Lea, 1856 by original designation.
- Contradens Haas, 1911: pl. 18. Type species: Unio contradens Lea, 1838 by original designation.



Fig. 7. (A) UPGMA dendrogram of freshwater ecoregion Contradentini+Rectidentini assemblages. (B) MNDS plot of phylogenetic β diversity (UniFrac) between drainages/landmass assemblages. (C) Map of the South-east Asian subregion and its constituent freshwater ecoregions and provinces. Freshwater ecoregions (Abell *et al.* 2008) without known records of the Contradentini+Rectidentini assumed to be part of the greater province are denoted by a lighter shade.

Taxon	Voucher (tissue)	SRR	Source
Contradentini			
Lens eximius	UF_507475 (ICH-02131)	SRR12439708	This study
Lens comptus	UF_507423 (ICH-00563)	SRR12439707	This study
Lens contradens	UF_507874 (ICH-02095)	SRR8473045	Pfeiffer et al. 2019
Lens inornatus	UF_507662 (2014-0706)	SRR12439696	This study
Lens maenamensis	UF_507382 (ICH-00416)	SRR12439695	This study
Lens micropterus	UF_507395 (ICH-00463)	SRR12439694	This study
Lens misellus	UF_507653 (2014-0686)	SRR12439693	This study
Lens pallegoixi	UF_507620 (2014-0615)	SRR12439692	This study
Physunio superbus	UF_507729 (ICH-00687)	SRR8473039	Pfeiffer et al. 2019
Physunio modelli	UF_507489 (ICH-02154)	SRR12439691	This study
Physunio pelluscidus	UF_507799 (ICH-00828)	SRR12439690	This study
Solenaia emarginata	UF 521836 (ICH-02397)	SRR8473074	Pfeiffer et al. 2019
Trapezoideus foliaceus	UF_507865 (ICH-02058)	SRR8473069	Pfeiffer et al. 2019
Trapezoideus subviridis	UF_507520 (ICH-02194)	SRR12439689	This study
Yaukthwa paiensis	UF_507709 (ICH-00640)	SRR8473071	Pfeiffer et al. 2019
Rectidentini			
Rectidens sumatrensis	BIV-1665	SRR8473077	Pfeiffer et al. 2019
Ensidens ingallsianus	UF_507686 (2012-0417)	SRR8473066	Pfeiffer et al. 2019
Ensidens dugasti	UF_507631 (2014-0647)	SRR12439706	This study
Ensidens spiculus	UF_507798 (ICH-00824)	SRR12439705	This study
Ensidens jaculus	UF_507405 (ICH-00514)	SRR12439704	This study
Ensidens telus	UF_507553 (ICH-02256)	SRR12439703	This study
Ensidens sagittarius	UF_507619 (2014-0610)	SRR12439702	This study
Hyriopsis bialata	UF_507433 (ICH-00592)	SRR8473061	Pfeiffer et al. 2019
Hyriopsis delaportei	UF_507425 (ICH-00567)	SRR12439701	This study
Hyriopsis khoratensis	UF_507467 (ICH-02117)	SRR12439700	This study
Hyriopsis kratiensis	UF_507402 (ICH-00502)	SRR12439699	This study
Hyriopsis myersiana	UF_507871 (ICH-02090)	SRR12439698	This study
Hyriopsis sakhonensis	UF_507786 (ICH-00803)	SRR12439697	This study
Lamprotulini			
Lamprotula cornuumlunae	UMMZ 304345 (20693.1a)	SRR8473058	Pfeiffer et al. 2019

Table 3. Taxa, vouchers, and source information for individuals includes in phylogenomic analyses

 Table 4.
 Summary statistics of the five concatenated AHE datasets

PIS, parsimony informative sites; GC content, guanine-cytosine content

Dataset	Loci and partitions	Length (nt)	Indels (%)	GC content (%)	PIS (%)
Heads	538	216104	6.9	28.0	28.4
Probes	538	105761	0.1	42.1	7.6
Tails	538	218266	6.9	27.8	28.0
Flanks (heads+tails)	1076	434370	6.9	27.9	28.2
Full sequences (heads+probes+tails)	1615	540131	5.6	30.7	24.1

- Schizocleithrum Haas, 1911: pl. 22. Type species: Unio pajakomboensis Bullen, 1906 by original designation.
- *Uniandra* Haas, 1913: 140. *Type species*: *Unio inaequalis* Rochebrune, 1882 by original designation.
- Sprickia Modell, 1942: 189. *Type species: Unio verbecki* von Martens, 1897 by original designation.

Diagnosis

Lens is a morphologically diverse clade (Fig. 11) but is distinguished from its sister taxon, *Solenaia*, by being much more circular or ovate, as opposed to being ultra-elongate

(Fig. 10). *Lens* often has some form of fine zig-zag umbo sculpture, distinguishing it from *Pressidens* (thick and wavy), and *Yaukthwa*, *Physunio* and *Trapezoideus* (faintly nodulous).

Distribution

Widespread in Indochina from the Salween drainage in the west to the Mekong drainage in the east. Also occurs on the Malay Peninsula and the islands of Sumatra, Java and Borneo.

Таха

We recognise 12 valid species in the genus Lens (Fig. 11).



Fig. 8. (A) Distribution of each individual locus length and the fraction of shared bipartitions between individual gene trees and the fully concatenated tree. (B) Distribution of each individual locus GC content and proportion of parsimony-informative sites per locus.

- Lens eximius (Lea, 1856).
- Lens comptus (Deshayes in Deshayes and Jullien 1876), comb. nov.
- Lens contradens (Lea, 1838), comb. nov.
- Lens inornatus (Lea, 1856), comb. nov.
- Lens lugens (Drouët & Chaper, 1892), comb. nov.
- Lens maenamensis, sp. nov.
- Lens micropterus (Morelet, 1866), comb. nov.
- Lens misellus (Morelet, 1865), comb. nov.
- Lens pallegoixi (Sowerby, 1867), comb. nov.
- *Lens rolfbrandti* (Jeratthitikul & Panha in Jeratthitikul *et al.* 2019), **comb. nov.**

- Lens semmelinki (von Martens, 1891), comb. nov.
- Lens novoselovi (Konopleva, Bolotov, Spitsyn, Kondakov, Gofarov & Vikhrev, 2019), comb. nov.

Remarks

Specimens representative of the taxon *Unio eximius* Lea, 1856 were recently recovered within the genus *Contradens* and the nominal species was revised to *Contradens eximius* (Lea, 1856) (Bolotov *et al.* 2017*b*). However, *Unio eximius* Lea, 1856 is the type species of *Lens* Simpson, 1900, and that genus has priority over *Contradens* Haas, 1911. Although resurrecting the generic



Fig. 9. ML reconstruction of the fully concatenated dataset (Probes+Flanks = 1614 loci). Coloured boxes indicate nodal support of six analyses: green – >95 UFBoot/ASTRAL PP; yellow – 68–94 UFBoot; red – clade not recovered.

status of *Lens* introduces many novel combinations, it is clearly the senior synonym of *Contradens*.

Uniandra subcircularis Brandt, 1974 has often been attributed to Contradens (=Lens) (Brandt 1974; Graf and Cummings 2007; Zieritz *et al.* 2018*a*; Jeratthitikul *et al.* 2019), but based on its strongly circular shape and robust cardinal teeth this species may belong to Leoparreysia (Parreysiinae: Leoparreysiini) (Pfeiffer *et al.* 2018*a*; Konopleva *et al.* 2019*a*). This hypothesis has yet to be tested but appears to have important implications regarding the distribution and dispersal of the Leoparreysiini, which is otherwise not known to be distributed east of the Salween drainage.

Unio gratiosus Philippi, 1843 has also been attributed to *Contradens* (=*Lens*) (Graf and Cummings 2007; Zieritz *et al.* 2018*a*; Konopleva *et al.* 2019*a*) but the shell disc of that putative species has an abundance of very fine shell sculpture which is unlike any other species of *Lens*, and more closely

resembles the sculpturing common among representatives of the Indochinellini (Parreysiinae). We tentatively place this poorly known species in the genus *Radiatula* as *?Radiatula gratiosus* (Philippi, 1843) **comb. nov.**

Lens is one of only two genera in the Contradentini +Rectidentini that have representatives distributed in the Lower & Middle Salween ecoregion and the ecoregions to the east, the other genus being *Trapezoideus*. All known Lens species are distributed east of the Salween drainage except Lens contradens, which is also found primarily east of the Salween but occurs in one small portion of the Salween drainage, the Moei watershed. This disjunction suggests that part of the Moei watershed was once part of the Mae Klong or Chao Phraya drainage and was subsequently captured by the Salween, causing at least part of the Thai Gulf province fauna to be integrated into the Salween drainage. Lens contradens individuals occurring on either side of this important



Fig. 10. Representatives of the genera of the Contradentini and Rectidentini.

biogeographic barrier are molecularly very similar, suggesting that this putative capture event occurred recently (Fig. 12). This recent stream capture is also supported by the disjunct distributions and shallow molecular divergences of the freshwater fish *Paracanthocobitis zonalternans* and *Schistura auranantiaca* in the Moei (Salween drainage) and Khwae Yai (Mae Klong drainage), and has been estimated to have occurred 1.5 million years ago (Bohlen *et al.* 2020*a*, 2020*b*). Similar to our phylogenomic reconstruction (Fig. 9) but with greater taxon sampling, our *COI* phylogeny shows a diverse radiation of at least six *Lens* species, all of which are endemic to the Mekong drainage (Fig. 12). This pattern of high genetic divergence in and around the Khorat plateau is a recurring pattern and is found in at least three other clades of the Contradentini+Rectidentini. In contrast to this geographically restricted and genetically divergent Mekong radiation is *L. contradens*, which is



Fig. 11. Representative individuals of each species of *Lens*. Scale bar equals 1 inch (2.54 mm) (size approximated for bottom three specimens). Image of *Lens novoselovi* reproduced from Konopleva *et al.* (2019*b*).

distributed across much of western South-east Asia and shows very little geographic structuring (Fig. 12). These clades are closely related but have dramatically different phylogeographic patterns.

Lens eximius (Lea, 1856)

(Tables 1, 3; Fig. 1, 9–13; Tables S1, S2; Fig. S1–S5)

- Unio eximius Lea, 1856, p. 93 figured in Lea 1857, p. 294, pl. 25, fig. 8. Type locality: 'Siam' [Thailand, not fixed]. Type(s): lectotype, USNM 83900 (Johnson 1974, p. 54, as the holotype).
- Unio semiquadrata Sowerby, 1866: unpaginated, pl. 48, fig. 258. Type locality: 'Camboja, Lao Mountains' [North-eastern Cambodia?]. Type(s): syntypes, NHMUK 1968658 (n = 3).

Taxonomic opinions since Haas (1969a)

Physunio (s.s.) eximius - Haas (1969a, p. 89).

Physunio (Lens) eximius - Haas (1969b, N428, fig. D28:8).

- Physunio eximius Brandt (1974, p. 295, pl. 25, fig. 58), Sri-aroon et al. (2007, p. 298), Graf and Cummings (2007, p. 311), He and Zhuang (2013, p. 86, fig. 205–208), Pfeiffer and Graf (2015, p. 315), Bolotov et al. (2017a, p. 12, table S1), Zieritz et al. (2018a, online table 1).
- *Contradens eximius* Bolotov *et al.* (2017*b*, table S1), Bolotov *et al.* (2018, table S1), Konopleva *et al.* (2019*a*, table S2; 2019*b*, p. 25), Huang *et al.* (2019, table S4), Zieritz *et al.* (2020, p. 2242), Bolotov *et al.* (2020, table S1).

Material examined

97 lots (Table S1).

Solenaia emarginatus



Fig. 12. COI gene tree of Lens. Nodal support (UFBoot) is listed above branches.

Diagnosis

Distinguished from other species of *Lens* by being very laterally compressed, having a broadly rounded or square posterior end, and a posterior wing that extends well above the umbo.

Distribution

Mekong drainage in eastern Thailand, central Laos, and westcentral Vietnam (Fig. 13).

Ecoregion

Khorat Plateau

Remarks

Most records are from the Mun watershed but extralimital populations occur as far north as Nakhon Phanom, Thailand, and as far east as Lao Bao, Vietnam. These geographically divergent populations are morphologically similar to the Mun River populations, but they have not been included in a molecular phylogeny. Research focused on these extralimital populations is



Fig. 13. Dot distribution map of Lens eximius, L. maenamensis and L. rolfbrandti.

warranted. This species has been referred to commonly as the Half Square (Sowerby 1866).

Lens comptus (Deshayes in Deshayes and Jullien 1876), comb. nov.

(Tables 1, 3; Fig. 1, 9, 11, 12, 14; Tables S1, S2; Fig. S1–S5)

Unio comptus Deshayes in Deshayes and Jullien 1876, p. 126, pl. 6, fig. 3-4. Type locality: 'Cambodge' [Cambodia, not fixed].

Type(s): syntype, MNHN-IM-2000–1661. *Remarks*: Label with syntype reads 'Peam Chelang, Cambodia' [Peam Chileang, Cambodia, 12.092116, 105.551361].

Harmandia munensis Brandt, 1974, p. 284, pl. 21, fig. 38. Type locality:
'Mun River at Pibun Mangsahan' [Mun River (Mekong Drainage), Phibun Mangsahan, Ubon Ratchathani Province, Thailand, 15.25006, 105.23728]. Type(s): holotype, SMF 220828 (Zilch 1983, p. 80). Remarks: Brandt (1974) called the holotype SMRL 5792/A in the text and SMF 220828 in the plate legend.



Fig. 14. Dot distribution map of Lens comptus, L. pallegoixi and L. novoselovi.

Taxonomic opinions since Haas (1969a)

Trapezoideus misellus [in part] – Haas (1969a, p. 76).

Trapezoideus exolescens comptus [in part] – Brandt (1974, p. 300, pl. 26, fig. 65).

Harmandia munensis – Brandt (1974, p. 284, pl. 21, fig. 38), Graf and Cummings (2007, p. 310), Zieritz *et al.* (2018*a*, online table 1).

Trapezoideus exolescens [in part] – He and Zhuang (2013, p. 121).

Contradens sp. 6 – Bolotov et al. (2017a, table S1).

Contradens sp. 'Nam Long' – Bolotov et al. (2017b, table S1).

Trapezoideus comptus – Pfeiffer *et al.* (2018*a*, p. 406, table 1).

Contradens comptus [in part] – Konopleva et al. (2019b, p. 25).

Contradens comptus – Konopleva *et al.* (2019*a*, p. 5), Zieritz *et al.* (2020, p. 2242), Bolotov *et al.* (2020, table S1).

Material examined

62 lots (Table S1).

Diagnosis

Distinguished from other species of *Lens* by its rectangular outline and finely sculptured posterior wing. Most similar to *L. pallegoixi* but has a less trapezoidal shell outline and lacks wrinkles on the ventral edge of the shell disc.

Distribution

Mekong drainage in eastern Thailand, Laos, north-western Vietnam, and Cambodia (Fig. 14).

Ecoregions

Lower Lancang, Khorat Plateau, Kratie-Stung Treng, and Mekong Delta.

Remarks

This species is geographically widespread and is typically found in or near the Mekong River proper and its larger tributaries (although see exceptions in northern Laos and north-western Vietnam) (Fig. 14). This type of distribution is reminiscent of patterns observed in some North American taxa commonly referred to as 'large river specialists' (Haag 2012). Although very little is known about the ecology of *L. comptus*, its distribution (Fig. 14) and limited genetic diversity (Fig. 12) suggest that this species may also have adaptations associated with a large river ecology, like being a host generalist or relying on highly vagile, large river host fishes (Berg *et al.* 2007; Roe and Boyer 2015; Pfeiffer *et al.* 2018*b*).

Lens contradens (Lea, 1838), comb. nov.

(Tables 1, 3; Fig. 1, 9, 11, 12, 15; Tables S1, S2; Fig. S1–S5)

- *Unio contradens* Lea, 1838, p. 75, pl. 18, fig. 58. *Type locality*: 'Java' [Java, Indonesia, not fixed]. *Type(s)*: holotype by monotypy, USNM 85185 (Johnson and Baker 1973, p. 151).
- Unio javanus Lea, 1840, p. 285 figured in Lea 1842, p. 220, pl. 18, fig. 37. *Type locality*: 'Java' [Java, Indonesia, not fixed]. *Type(s)*: holotype by monotypy, USNM 85187 (Johnson 1974, p. 77).
- *Unio exilis* Dunker, 1846, p. 109 figured in Mousson 1849, p. 92, pl. 16, fig. 3. *Type locality*: 'Ins. Java' [Java, Indonesia, not fixed]. *Type(s)*: unknown.
- Unio mutatus Mousson, 1849, p. 92, pl. 16, fig. 1–2. *Type locality*: 'Pardana und Tjikoya' [Java. Not fixed]. *Type(s)*: unknown.

- Unio tumidulus Lea, 1856 (non Locard, 1889), p. 93 figured in Lea 1857, p. 295, pl. 25, fig. 9. *Type locality*: 'Siam' [Thailand, not fixed]. *Type(s)*: lectotype, USNM 84712 (Johnson 1974, p. 149, as the holotype).
- Unio cambodiensis Lea, 1856, p. 103 figured in Lea 1857, p. 313, pl. 30, fig. 28. *Type locality*: 'Tackrong River at Korat, Cambodia' [Takhong River (Mekong Drainage), near Korat, Nakhon Ratchasima Province, Thailand, 14.98216, 102.04172]. *Type(s)*: lectotype, USNM 84909 (Johnson 1974, p. 26, as the holotype). *Remarks*: See the Remarks section of *Lens contradens* about the questionable accuracy of this type locality.
- Unio ascia Hanley, 1856, p. 385, pl. 23, fig. 20. Type locality: 'Penang' [Penang Island, Malaysia, 5.41476, 100.34762]. Type(s): lectotype, MCZ 17046 (Johnson 1956, p. 106). Remarks: Attributed by Hanley to 'Benson, MS'.
- *Unio rusticus* Lea, 1856 (non Sowerby, 1868), p. 93 figured in Lea 1857, p. 294, pl. 25, fig. 7. *Type locality*: 'Siam' [Thailand, not fixed]. *Type(s)*: lectotype, USNM 84082 (Johnson and Baker 1973, p. 169, as the holotype).
- Unio sumatrensis Lea, 1859 (non Dunker, 1853), p. 153 figured in Lea 1860a, p. 239, pl. 34, fig. 118. *Type locality*: 'Sumatra' [Sumatra, Indonesia, not fixed]. *Type(s)*: lectotype, USNM 84059 (Johnson and Baker 1973, p. 172, as the holotype). *Remarks*: Junior primary homonym of Unio sumatrensis Dunker, 1852. Re-named Unio dimotus Lea, 1870.
- Unio mederianus Küster, 1861, p. 242, pl. 80, fig. 7. Type locality: 'Insel Java' [Java, Indonesia, not fixed]. Type(s): unknown. Remarks: Attributed by Küster to 'Mousson'.
- Unio paivanus Morelet, 1865, p. 227. Type locality: 'Siam' [Thailand, not fixed]. Type(s): lectotype, NHMUK 1893.2.4.1738 (Johnson 1971, p. 90, as the holotype). Remarks: Label with lectotype reads 'Saraburi River, Siam' [Pa Sak River (Chao Phraya Drainage), Thailand].
- Unio asperulus Lea, 1866, p. 133 figured in Lea 1868, p. 280, pl. 38, fig. 94. Type locality: 'Siam' [Thailand, not fixed]. Type(s): lectotype, USNM 84078 (Johnson 1974, p. 17, as the holotype).
- Unio dimotus Lea, 1870, p. 30. Remarks: Replacement name for Unio sumatrensis Lea, 1859.
- Unio semidecoratus Morlet, 1889, p. 164, 192, pl. 8, fig. 4. Type locality: 'Rivière de Srakéo, à Srakéo (Siam)' [Srakeo River (=Klong Phra Sathueng) (Bang Pakong Drainage), Sa Kaeo, Sa Kaeo Province, Thailand, 13.80952, 102.05481]. Type(s): unknown.
- Unio dautzenbergi Morlet, 1889, p. 163, 190, pl. 8, fig. 5. Type locality: 'Rivière de Srakéo, à Srakéo (Siam)' [Srakeo River (=Klong Phra Sathueng) (Bang Pakong Drainage), Sa Kaeo, Sa Kaeo Province, Thailand, 13.80952, 102.05481]. Type(s): unknown.
- Unio verbecki von Martens, 1897, p. 89, pl. 5, fig. 1–2, 4–5. *Type locality*: 'Sumatra: See von Singkarah' [Singkarak Lake, Sumatera Barat, West Sumatra, Indonesia, –0.62196, 100.54390]. *Type(s)*: syntype, ZMA. MOLL.139133. *Remarks*: Attributed to 'Bött.' by von Martens.
- Unio hageni Strubell, 1897, p. 10. Type locality: 'Südsumatra' [Southern Sumatra, Indonesia, not fixed]. Type(s): holotype, SMF 3603 (Zilch 1967, p. 91, as SMF 13849).
- Unio laticeps von Martens, 1900, p. 15. Type locality: 'See Danau Baru, Indragiri' [Indragiri River, Danau Baru, Riau Province, Sumatra, Indonesia, -0.33196, 102.40482]. Type(s): syntypes, ZMB 51796 (n = 2).
- Trapezoideus peninsularis Simpson, 1900, p. 859. Type locality: 'Sumatra' [Sumatra, Indonesia, not fixed]. Type(s): holotype, NHMUK 1964159 (Johnson 1971, p. 17). Remarks: Simpson (1900, p. 859) stated that this was not Unio sumatrensis Lea, 1859 or Unio sumatrensis Dunker, 1852 and based his name T. peninsularis on Reeve's figure (pl. 28, fig. 142) of Unio sumatrensis 'Lea'.
- Unio pajakomboensis Bullen, 1906, p. 15, pl. 2, fig. 9–11. Type locality: 'Pajakombo' [Payakumbuh, (Indragiri Drainage), Sumatera Barat,

Sumatra, Indonesia, -0.23333, 100.63333]. *Type(s)*: lectotype, NHMUK 1906.1.16.52 (Johnson 1971, p. 90, as the holotype).

- Unio thaiensis Habe, 1964, p. 62, pl. 1, fig. 3–4. Type locality: 'Borapet Swamp' [Bueng Boraphet, Nakhon Sawan Province, Thailand, 15.718378, 100.208234]. Type(s): unknown. Remarks: Habe mentions a 'type' and two 'paratypes,' and in the introduction he says, 'Some specimens were also donated to the National Science Museum, Tokyo through Mr. C. Amatayakul of the Fisheries Department at Bangkok.'
- Uniandra contradens rusticoides Brandt, 1974, p. 290, pl. 24, fig. 50. Type locality: 'Klong Min near Chandi, Chawang' [Klong Min (Tapi Drainage), near Chandi, Chawang, Nakhon Si Thammarat Province, Thailand, 8.40280, 99.50385]. Type(s): holotype, SMF 220845 (Zilch 1983, p. 81). Remarks: Brandt (1974) called this SMRL 2435/A in the text and SMF 220845 in the plate legend.

Taxonomic opinions since Haas (1969a)

- *Contradens contradens* Haas (1969a, p. 97), Graf and Cummings (2006a, p. 348), Graf and Cummings (2007, p. 310), Whelan *et al.* (2011, p. 506), Affandi *et al.* (2014, p. 113, fig. 2B), Pfeiffer and Graf (2015, p. 310), Zieritz *et al.* (2016, p. 1071), Lopes-Lima *et al.* (2017, p. 177), Bolotov *et al.* (2017*a*, p. 12, table S1; 2017*b*, table S1), Konopleva *et al.* (2017, p. 207), Zieritz *et al.* (2018*a*, online table 1), Bolotov *et al.* (2018, table S1), Razak *et al.* (2019, p. 459), Pfeiffer *et al.* (2018*a*, p. 410), Konopleva *et al.* (2019*a*, table S2; 2019*b*, p. 30), Huang *et al.* (2019, table S4), Pfeiffer *et al.* (2019, p. 116), Zieritz *et al.* (2020, table S1), Lopes-Lima *et al.* (2020, table 1).
- Contradens contradens [in part] Do *et al.* (2018, p. 5, table 2), Jeratthitikul *et al.* (2019, p. 140, fig. 1.1–1.6).

Ensidens ingallsianus [in part] - Woodward (1969, p. 49).

Ensidens (s.s.) ingallsianus [in part] - Haas (1969a, p. 72).

Ensidens (Uniandra) inaequalis [in part] - Haas (1969a, p. 73).

Ensidens (Uniandra) asperulus [in part] - Haas (1969a, p. 74).

Physunio (s.s.) cambodiensis – Haas (1969a, p. 89).

- Contradens semmelincki [sic] [in part] Haas (1969a, p. 97).
- Contradens ascia [in part] Haas (1969a, p. 99).
- Contradens rusticus [in part] Haas (1969a, p. 100).
- Contradens dautzenbergi Haas (1969a, p. 100).
- Contradens verbeeki [sic] Haas (1969a, p. 101).
- Contradens hageni Haas (1969a, p. 101).
- Contradens (s.s.) contradens Haas (1969b, N420, fig. D20:4).
- Contradens (Sprickia) verbeeki [sic] Haas (1969b, N420, fig. D20:6).

Uniandra contradens contradens – Brandt (1974, p. 289).

Uniandra contradens tumidula [in part] – Brandt (1974, p. 290, pl. 24, fig. 51–52).

- *Physunio cambodiensis* Brandt (1974, p. 297, pl. 25, fig. 61), Sri-aroon *et al.* (2007, p. 298), Graf and Cummings (2007, p. 311), Zieritz *et al.* (2018*a*, online table 1), Do *et al.* (2018, p. 10, table 2), Konopleva *et al.* (2019*a*, table S2).
- Uniandra contradens ascia Brandt (1974, p. 289, pl. 24, fig. 49).
- Uniandra contradens dimotus Brandt (1974, p. 289).
- Uniandra contradens rusticoides Brandt (1974, p. 290, pl. 24, fig. 50). Uniandra contradens rustica [in part] – Brandt (1974, p. 291, pl. 24, fig. 53).
- Contradens ascia dimotus Marwoto (1987, p. 306).

Uniandra contradens - Graf (2002, p. 66), Hoeh et al. (2009, p. 310).

Uniandra contradens [in part] – Bogan and Do (2014, p. 113).

Trapezoideus peninsularius [sic] - Graf and Cummings (2007, p. 312).

Contortus [sic] contortus [sic] – Araujo et al. (2017, p. 280).

Trapezoideus peninsularis – Zieritz et al. (2018a, online table 1).

Contradens peninsularis – Konopleva et al. (2019a, p. 4, table S2; 2019b, p. 25).

Material examined

375 lots (Table S1).

Diagnosis

Distinguished from other species of *Lens* by its ovate shell outline, moderate inflation, and a tendency to have thick concentric wrinkles across the shell disc. Most similar to *L. rolfbrandti* but is less subtriangular and elongate, and more ovate and truncate.

Distribution

Widespread in the Chao Phraya and Mae Klong drainages in western and central Thailand, as well as the smaller coastal drainages of south-eastern Thailand, Malay Peninsula, Sumatra, and Java (Fig. 15). Nearly absent from the Mekong and Salween drainages; known only from a few geographically disjunct populations in the Mekong (Kok, Ing, Loei watersheds) and Salween (Moei watershed).

Ecoregions

Lower & Middle Salween, Mae Klong, Chao Phraya, Eastern Gulf of Thailand Drainages, Lower Lancang, Northern Central Sumatra–Western Malaysia, Malay Peninsula Eastern Slope, Southern Central Sumatra, Southern Sumatra & Western Java, and Central & Eastern Java.

Remarks

We consider the nominal species U. cambodiensis Lea, 1856 a junior synonym of L. contradens based on its strongly similar shell characteristics. This taxonomic hypothesis is somewhat problematic in that U. cambodiensis was described from 'Tackrong River at Korat, Cambodia' and with some interpretation most likely refers to Lam Takhong near Nakhon Ratchasima, Thailand, which is in the Mun watershed (Mekong drainage) and outside the known distribution of L. contradens (Fig. 15 - dot with "?"). However, the type locality of U. cambodiensis is unexpectedly precise in comparison to the other type material sent to Issac Lea from William Haines, and it may be dubious. The type of U. cambodiensis Lea, 1856 and at least 15 other type specimens were sent to Issac Lea by William Haines and the locality for each of these types, except Unio cambodiensis, was 'Siam'. The surprising precision of the type locality of U. cambodiensis raises suspicion about its accuracy. However, some of the material sent to Lea by Haines can be deduced to have come from the Mekong drainage because several of these nominal species are endemic to that drainage (e.g. U. eximius, U. phaselus, U. humilis, U. sagittarius).

Lens contradens is one of the most geographically widespread Contradentini in South-east Asia, occurring in at least 11 ecoregions. Its current distribution (Fig. 15) and limited genetic diversity (Fig. 12) appears to be driven, at least in part, by the increased hydrological connectivity associated with Pleistocene sea level lowering and the formation of several large palaeodrainages on Sundaland (Voris 2000). The Paleo Siam River joined many drainages



Fig. 15. Dot distribution map of Lens contradens, L. micropterus, L. lugens and L. semmelinki.

of the modern Gulf of Thailand (e.g. Mae Klong, Chao Phraya, Bang Pakong, Chantaburi, smaller coastal rivers of eastern Malay Peninsula) and represents most of the *L. contradens* distribution. The species also appears to have been influenced by the Paleo Malacca Straits River and Paleo East Sunda River, although these populations have not been thoroughly assessed in a phylogenetic context.

Despite its wide distribution, the species is nearly absent from two of the largest drainages in modern-day South-east Asia, the Mekong and Salween, both of which are not typically associated with the Paleo Siam drainage. In both the Salween and Mekong drainages, *L. contradens* is restricted to just a small fraction of these much larger drainages. These four disjunct populations appear to be the products of stream capture events between these adjacent drainages (see arrows in Fig. 15). Each of the isolated populations in the Mekong (Kok, Ing, Loei) and Salween (Moei) drainages are restricted to relatively small watersheds that generally flow from south to north, the opposite direction in comparison to the drainage's general flow, creating drainage network geometries that are often characteristic of stream capture (Bishop 1995). All three of the Mekong tributaries, the Kok, Ing and Loei, have been previously hypothesised as areas of drainage rearrangement (Hutchison 1989; Rainboth *et al.* 2012), and the Moei has

recently been hypothesised to have captured the upper reaches of the Mae Klong (Bohlen *et al.* 2020a, 2020b). The molecular divergences between the Mekong and Chao Phraya samples and Salween and Chao Phraya samples are very shallow, suggesting that the stream captures are recent (Fig. 12). The Lower Lancang and Middle & Lower Salween ecoregions are much more poorly sampled in comparison to other parts of the distribution of *L. contradens* (Fig. 3) so increased sampling in those ecoregions will be useful in better understanding the distribution of this species in the Mekong and Salween and the number of putative stream-capture events.

Lens contradens is only one of two species in the Contradentini thought to occur in both mainland South-east Asia and the Malay Archipelago (the other being Physunio superbus). However, no L. contradens population from the Malay Archipelago has been included in a phylogenetic analysis (Fig. 15) and their conspecific nature is based solely on their shared morphological similarities. Including putative L. contradens individuals from the Malay Archipelago in a phylogenetic analysis is an important research priority, especially considering the type locality of Unio contradens is 'Java' and the importance of these populations in understanding palaeodrainage evolution. Furthermore, there are two putative Lens species endemic to the Malay Archipelago, L. lugens and L. semmelinki, that are also morphologically very similar to L. contradens and may be junior synonyms, but these taxa have also not been included in a molecular phylogeny.

Lens inornatus (Lea, 1856), comb. nov.

(Tables 1, 3; Fig. 1, 9, 11, 12, 16; Tables S1, S2; Fig. S1–S5)

Unio inornatus Lea, 1856, p. 93 – figured in Lea 1857, p. 296, pl. 24, fig. 6. *Type locality*: 'Siam' [Thailand, not fixed]. *Type(s)*: lectotype, USNM 85196 (Johnson 1974, p. 74, as the holotype).

Taxonomic opinions since Haas (1969a)

Physunio (s.s.) inornatus - Haas (1969a, p. 88).

Physunio inornatus – Brandt (1974, p. 295, pl. 25, fig. 59), Graf and Cummings (2007, p. 311), Kongim *et al.* (2015, p. 98), Zieritz *et al.* (2018*a*, online table 1), Konopleva *et al.* (2019*a*, table S2).

Material examined

25 lots (Table S1).

Diagnosis

Distinguished from other species of *Lens* by having a very thin shell and delicate teeth. Most similar to *Trapezoideus* foliaceus but is more elongate, dorso-ventrally shorter, and has a more round posterior end.

Distribution

Mae Klong, Chao Phraya, and Bang Pakong drainages in western and central Thailand (Fig. 16).

Ecoregions

Mae Klong, Chao Phraya.

Remarks

Occurs sympatrically with *Trapezoideus* foliaceus and can be very difficult to distinguish morphologically. *Trapezoideus* foliaceus tends to be the more common of the two species and is dorso-ventrally taller. Despite the large geographic distances between the sequenced individuals in the Chao Phraya and Mae Klong drainages, the sampled populations are genetically very similar, suggesting recent population expansion that may be associated with the Paleo Siam River (Fig. 12, 16).

Lens lugens (Drouët & Chaper, 1892), comb. nov.

(Table 1; Fig. 1, 11, 15; Table S1)

- Unio lugens Drouët & Chaper, 1892, p. 147, pl. 5, fig. 1–3. Type locality: 'Le Kapoeas (Semitau), à Borneo' [Kapuas River, Semitau, West Kalimantan Province, Borneo, Indonesia, 0.55548, 111.96045]. Type(s): syntypes, MCZ 174097 (n = 2) (Johnson 1956, p. 123, as paratypes), MNHN-IM-2000–1739 (n = 1).
- Unio saccellus Drouët & Chaper, 1892, p. 148, pl. 5, fig. 4–6. Type locality:
 'Sebroeang, à Bornéo' [Soengai Sebroeang (Kapuas Drainage), Sebroeang, West Kalimantan Province, Borneo, Indonesia, 0.43333, 111.88333]. Type(s): syntypes, MCZ 174095 (n = 1) (Johnson 1956: 133, as a paratype); MNHN-IM-2000–1774 (n = 1).
- Unio fulvaster Drouët & Chaper, 1892, p. 154, pl. 6, fig. 11–13. Type locality:
 'Kapoeas (Semitau), à Bornéo' [Kapuas River, Semitau, West Kalimantan Province, Borneo, Indonesia, 0.55548, 111.96045].
 Type(s): holotype by monotypy, MNHN-IM-2000-1701.

Taxonomic opinions since Haas (1969a)

Contradens ascia [in part] - Haas (1969a, p. 99).

Contradens fulvaster – Haas (1969*a*, p. 98), Graf and Cummings (2007, p. 310), Zieritz *et al.* (2018*a*, online table 1), Konopleva *et al.* (2019*a*, table S2; 2019*b*, p. 25), Zieritz *et al.* (2020, p. 2237).

Material examined

31 lots (Table S1).

Diagnosis

Unknown

Distribution

Kapuas drainage in Borneo (Fig. 15).

Ecoregion

Kapuas.

Remarks

The validity of this taxon is uncertain - it may be a junior synonym of *L. contradens*. The species has not yet been included in a molecular phylogeny.

Lens maenamensis, sp. nov.

(Tables 1, 3; Fig. 1, 9, 11–13; Tables S1, S2; Fig. S1–S5)

Type locality

Tonle Srepok River, Highway 78 bridge between Stung Treng and Ban Lung, Stung Treng Province, Cambodia, 13.54504, 106.01353.



Fig. 16. Dot distribution map of *Lens inornatus* and *Lens misellus*.

Types

Holotype, UF 564749. Paratypes, UF 507392 (n = 5), same locality as the holotype.

Taxonomic opinions since Haas (1969a)

Uniandra contradens tumidula [in part] – Brandt (1974, p. 290). Uniandra contradens crossei [in part] – Brandt (1974, p. 292, pl. 24, fig. 54). Contradens crossei [in part] – Jeratthitikul *et al.* (2019, p. 140, fig. 1.7–1.9). Contradens crossei – Konopleva *et al.* (2019*b*, p. 30), Bolotov *et al.* (2020, table S1). Material examined 46 lots (Table S1).

Diagnosis

Shell characteristics similar to *L. contradens* but tends to be more elongate and bluntly pointed.

Description

Shell morphology highly variable, compressed, ovate, and thin-shelled (especially in southern populations) to inflated,

circular, and thick-shelled (especially in northern populations). Periostracum, yellowish-brown to brown, often with 2-3 green rays on the posterior slope. Faint, wide, wavy sculpturing on the posterior slope and shell disc (especially in northern populations). Pseudocardinal and lateral teeth nearly parallel, blade-like. Left valve with two lateral teeth, long, slightly curved, diverging. Left valve with one long pseudocardinal tooth, small triangular swelling at posterior end. Right valve with one lateral tooth, long, slightly curved. Right valve with two pseudocardinal teeth, ventral tooth much larger than dorsal, with small triangular swelling at posterior end. Umbo shallow. Nacre iridescent, very faintly purplishblue, and translucent. Pallial fusion between supra-anal and excurrent larger than supra-anal aperture. Excurrent aperture smooth, shorter than incurrent. Incurrent aperture with multiple rows of long simple papillae. Demibranchs perforated. Interior demibranch attached to visceral mass only anteriorly. Ectobranchous brooding, marsupium laterally swollen, blush when glochidia are fully developed. Bilaterally asymmetrical glochidia.

Distribution

Mekong drainage in Laos, Thailand and Cambodia. Populations concentrated near the confluences of the Songkhram and the Mekong, and the Sekong and the Mekong (Fig. 13).

Ecoregions

Khorat Plateau, Kratie-Stung Treng.

Remarks

Jeratthitikul *et al.* (2019) recently recovered this molecular clade and resurrected the name *Contradens crossei*. However, other than the type specimen of *U. crossei*, Jeratthitikul *et al.* (2019) did not consider any *Contradens* (=*Lens*) specimens from the southern half of the Mekong drainage (see their Fig. 2). The omission of the available specimen data (i.e. museum specimens and molecular data) from this region compromised several of their hypotheses. More inclusive sampling of *Lens* from the Mekong drainage suggests that *U. crossei* is a junior synonym of *L. micropterus* (Morelet, 1866), and *C. crossei sensu* Jeratthitikul *et al.* (2019) represents a previously undescribed species (=*L. maenamensis*).

Jeratthitikul et al. (2019) resurrected C. crossei for a divergent molecular clade restricted to north-eastern Thailand. However, the type locality of Unio crossei Deshayes in Deshayes and Jullien 1876 is 'Cambodge' and is likely quite geographically distant from their closest samples in north-eastern Thailand. We collected Lens specimens from across Cambodia and found many specimens resembling the types of U. crossei and U. micropterus Morelet, 1866, which were molecularly very similar. Based on these findings we hypothesise that U. crossei is a junior synonym of Unio micropterus and the clade referred to as C. crossei in Jeratthitikul et al. (2019) represents a new species, L. maenamensis. Furthermore, our more inclusive taxon sampling of Lens demonstrates that L. rolfbrandti and L. maenamensis are quite distantly related to L. contradens, and the reported monophyly of these taxa is entirely artificial and a product of incomplete taxon sampling. As such, the biogeographic interpretation predicated on that hypothesis should be reconsidered.

Lens maenamensis is composed of two molecularly divergent clades, one is restricted to the Khorat Plateau and the other to the Kratie–Stung Treng ecoregion (Fig. 12). These two geographically disjunct clades appear to have some morphological disparities – the southern clade is more elongate and has a bluntly pointed posterior end while the northern population is more circular and broadly rounded and tends to have wide, wavy sculpturing on the shell disc. These divergent populations may represent distinct species, but further research is necessary.

Lens micropterus (Morelet, 1866), comb. nov.

(Tables 1, 3; Fig. 1, 9, 11, 12, 15; Tables S1, S2; Fig. S1–S5)

- *Unio micropterus* Morelet, 1866, p. 63 figured in Morelet 1875, p. 349, pl. 15, fig. 6 [7]. *Type locality*: 'in torrentibus montanis Cambodiæ' [The mountains of Cambodia, not fixed]. *Type(s)*: lectotype, NHMUK 1893.2.4.1596 (Johnson 1971, p. 88, as the holotype).
- *Unio cambojensis* Sowerby, 1866, unpaginated, pl. 42, fig. 231. *Type locality*: 'Camboja' [Cambodia, not fixed]. *Type(s)*: lectotype, NHMUK 1965148 (Johnson 1971, p. 80, as the holotype).
- Margaron (Unio) versus Lea, 1870, p. 46. Type locality: 'Cambojia' [Cambodia, not fixed]. Type(s): lectotype, NHMUK uncatalogued (Johnson 1971, p. 86). Remarks: Based upon Reeve's figure of Unio inornatus 'Hanley, MS', pl. 29, fig. 147.
- Unio crossei Deshayes in Deshayes and Jullien 1876, p. 124, pl. 6, fig. 5–7. Type locality: 'Cambodge' [Cambodia, not fixed]. Type(s): syntypes, MNHN-IM-2000–1668 (n = 8).
- Unio semialatus Deshayes in Deshayes and Jullien 1876, p. 123, pl. 6, fig. 1–2. *Type locality*: 'Peam Chelang, Cambodge' [Peam Chileang, Cambodia, 12.092116, 105.551361]. *Type(s)*: syntype, MNHN-IM-2000–1780 (n = 1/2).
- Diplodon ludovicianum Rochebrune, 1882, p. 43. Type locality: 'Preck-Scholl Haut Mekong' [Preck-Scholl, upper Mekong, not located]. Type(s): syntypes, MNHN-IM-2000–35806 (n = 4).
- Unio inaequalis Rochebrune, 1882, p. 44. Type locality: 'Rapides de Sombor' [Mekong River, Sombour, Sambour District, Kratié Province, Cambodia, 12.77440, 105.96311]. Type(s): unknown.
- Unio fischerianus Morlet, 1883, p. 109, pl. 4, fig. 6. Type locality: 'Cambodge' [Cambodia, not fixed]. Type(s): syntype, MNHN-IM-2000–1697.
- Unio siamensis Morlet, 1889 (non Lea, 1866), p. 164, 194, pl. 7, fig. 2. Type locality: 'Rivière de Sutrang' [Sutrang River, (Mekong Drainage), Ka Saeo Province, Thailand, 13.68877, 102.49712]. Type(s): lectotype, MNHN-IM-2000–33677, here designated. Remarks: Junior primary homonym of Unio siamensis Lea, 1866. Re-named Unio soboles Fischer, 1891.
- Unio soboles Fischer, 1891, p. 143. Remarks: Replacement name for Unio siamensis Morlet, 1889.

Taxonomic opinions since Haas (1969a)

Ensidens (Uniandra) inaequalis [in part] – Haas (1969a, p. 73).

- Ensidens (Uniandra) asperulus [in part] Haas (1969a, p. 74).
- Trapezoideus ludovicianus Haas (1969a, p. 75).
- Physunio (s.s.) micropterus Haas (1969a, p. 87).
- Physunio (s.s.) semialatus Haas (1969a, p. 88).
- Contradens crossei Haas (1969a, p. 98).
- Contradens ascia [in part] Haas (1969a, p. 99).
- Contradens rusticus [in part] Haas (1969a, p. 100).

Ensidens (Uniandra) inaequali – Haas (1969b, N423, fig. D21:6). Uniandra contradens tumidula [in part] - Brandt (1974, p. 290). Uniandra contradens rustica [in part] - Brandt (1974, p. 291). Uniandra contradens crossei [in part] - Brandt (1974, p. 292, pl. 24, fig. 54). Uniandra contradens fischeriana - Brandt (1974, p. 292, pl. 24, fig. 55). Physunio micropterus - Brandt (1974, p. 296, pl. 25, fig. 60), Graf and Cummings (2007, p. 311), Zieritz et al. (2018a, online table 1), Do et al. (2018, p. 10, table 2), Konopleva et al. (2019a, table S2). Trapezoideus exolescens comptus [in part] - Brandt (1974, p. 300). Contradens inaequalis - Graf and Cummings (2007, p. 310), Zieritz et al. (2018a, online table 1), Konopleva et al. (2019a, table S2). Physunio semialatus - Graf and Cummings (2007, p. 311). Trapezoideus exolescens [in part] – He and Zhuang (2013, p. 121). Uniandra contradens [in part] - Bogan and Do (2014, p. 114). Contradens contradens - Pfeiffer and Graf (2015, p. 310). Contradens contradens [in part] - Do et al. (2018, p. 5), Jeratthitikul et al. (2019, p. 135, fig. 1.6, 4). Contradens crossei [in part] – Jeratthitikul et al. (2019, p. 140, fig. 1.7–1.9). Contradens comptus [in part] - Konopleva et al. (2019a, p. 5).

Material examined

111 lots (Table S1).

Diagnosis

Distinguished from other species of *Lens* by its moderate sized wing, straight ventral margin, and moderate inflation.

Distribution

Mekong drainage in Thailand, Cambodia and Laos. Majority of records from the Cambodian Mekong (Fig. 15).

Ecoregion

Khorat Plateau, Kratie-Stung Treng, Mekong Delta.

Remarks

In the westernmost part of the L. micropterus distribution Tonle watershed) some specimens (i.e. Sap look morphologically identical sister to its species, L. contradens. Despite the strong morphological similarities to L. contradens these specimens maintain L. micropterus haplotypes. The Tonle Sap watershed is thought to be outside of the native range of L. contradens but given the economic importance of fisheries in the Tonle Sap (Hap et al. 2006), including non-native molluscs (Ngor et al. 2018), L. contradens may have been introduced and could be hybridising with L. micropterus. Further research is needed.

Lens misellus (Morelet, 1865), comb. nov.

(Tables 1, 3; Fig. 1, 9, 11, 12, 16; Tables S1, S2; Fig. S1–S5)

- Unio misellus Morelet, 1865, p. 21 figured in Morelet 1875, p. 34, pl. 14, fig. 2. *Type locality*: 'Siam' [Thailand, not fixed]. *Type(s)*: lectotype, NHMUK 1893.2.4.1593 (Johnson 1971, p. 88, as the holotype).
- Unio siamensis Lea, 1866, p. 133 figured in Lea 1868, p. 279, pl. 38, fig. 93. Type locality: 'Siam' [Thailand, not fixed]. Type(s): lectotype, USNM 85893 (Johnson and Baker 1973, p. 170, as the holotype).

Taxonomic opinions since Haas (1969a)

Trapezoideus misellus [in part] - Haas (1969a, p. 76).

Trapezoideus misellus – Dang *et al.* (1980, p. 507, hinh 311), Do *et al.* (2018, p. 12, Table 2).

Trapezoideus exolescens exolescens [in part] – Brandt (1974, p. 299), Subba Rao (1989, p. 195, fig. 556–557), Ramakrishna and Dey (2007, p. 328).

Trapezoideus exolescens [in part] – He and Zhuang (2013, p. 121).

Contradens misellus – Konopleva *et al.* (2019*a*, p. 7, table S2; 2019*b*, p. 25), Bolotov *et al.* (2020, table S1), Zieritz *et al.* (2020, p. 2242).

Material examined

14 lots (Table S1).

Diagnosis

Distinguished from other species of *Lens* by its strongly reduced dentition in adults. *Solenaia* also has dramatically reduced dentition but is easily distinguished from *L. misellus* by its ultra-elongate shell shape.

Distribution

Chao Phraya drainage in northern Thailand (Fig. 16).

Ecoregion

Chao Phraya.

Remarks

In adult specimens of *L. misellus* the pseudocardinal and lateral teeth are greatly reduced or absent, while young specimens have very fine but distinct teeth. This reduction in dentition is unusual among the Contradentini but also occurs in *Solenaia. Lens misellus* is also unusual in that it is the only Contradentini endemic to the Chao Phraya drainage.

Lens novoselovi (Konopleva, Bolotov, Spitsyn, Kondakov, Gofarov & Vikhrev, 2019), comb. nov.

(Table 1; Fig. 1, 11, 12, 14; Tables S1, S2)

Contradens novoselovi Konopleva et al., 2019, p. 26, fig. 1–3. Type locality: Tributary of Nam Fa River, near Vieng Phou Kha village, Laos, 20.68193, 101.07944. Type(s): holotype, RMBH biv 203_4. (RMBH = Russian Museum of Biodiversity Hotspots).

Taxonomic opinions since Haas (1969a)

Contradens sp. 7 – Bolotov et al. (2017a, table S1).

Contradens sp. 'Vieng Phou Kha' – Bolotov et al. (2017b, table S1), Konopleva et al. (2019a3B2 h -12pt?>, p. 2).

Contradens novoselovi – Konopleva et al. (2019b, p. 26, fig. 1–3), Bolotov et al. (2020, table S1).

Material examined

1 lot (Table S1).

Diagnosis

Lens novoselovi is thought to be distinguished from its sister species, *L. comptus*, by its smaller size, more ovate shell shape, more broadly rounded anterior margin, and less sculpturing on the posterior slope (Konopleva *et al.* 2019*b*).

Distribution

Known only from the type locality in the Mekong drainage, near Vieng Phou Kha, north-western Laos (Fig. 14).

Ecoregion

Lower Lancang.

Remarks

Lens novoselovi is the only species of the Contradentini or Rectidentini thought to be endemic to the Lower Lancang ecoregion. However, the Lower Lancang ecoregion is poorly characterised in comparison to the other Mekong ecoregions (Fig. 2, 3) and continued sampling in the region is likely to reveal greater species diversity (e.g. see Contradentini sp. account in problematic taxa section).

Lens pallegoixi (Sowerby, 1867), comb. nov.

(Tables 1, 3; Fig. 1, 9, 11, 12, 14; Tables S1, S2; Fig. S1–S5)

Anodon pallegoixi Sowerby, 1867, unpaginated, pl. 8, fig. 18. Type locality: 'Siam' [Thailand, not fixed]. Type(s): lectotype, NHMUK 1965193 (Johnson 1971, p. 90, as the holotype); paralectotypes NHMUK 1965194 (n = 2) (Johnson 1971, p. 90, as paratypes).

Taxonomic opinions since Haas (1969a)

Trapezoideus misellus [in part] – Haas (1969a, p. 76).

Trapezoideus exolescens pallegoixi – Brandt (1974, p. 300, pl. 26, fig. 64). *Trapezoideus exolescens* [in part] – He and Zhuang (2013, p. 121). *Contradens pallegoixi* – Konopleva *et al.* (2019*a*, p. 7, table S2; 2019*b*,

p. 25), Bolotov *et al.* (2020, table S1), Zieritz *et al.* (2020, p. 2242).

Material examined

30 lots (Table S1).

Diagnosis

Distinguished from other species of *Lens* by strong lateral compression, trapezoidal outline and, commonly, wrinkles on the ventral margin of the shell disc. Most similar to *L. comptus* but is less rectangular and more trapezoidal in shell outline.

Distribution

Mekong drainage in eastern Thailand (Fig. 14).

Ecoregion

Khorat Plateau.

Remarks

Despite many sampling events in the nearby Mekong River proper (Fig. 2), this species was never recovered and appears to be restricted to the Mun River watershed (Fig. 14).

Lens rolfbrandti (Jeratthitikul & Panha in Jeratthitikul *et al.* 2019), comb. nov.

(Table 1; Fig. 1, 11–13; Tables S1, S2)

Contradens rolfbrandti Jeratthitikul & Panha in Jeratthitikul et al. 2019, p. 141, fig. 1.11–1.12. *Type locality*: Huai Luang River at Don Kloi Village, Phibun Rak District, Udon Thani Province, Thailand, 17.47563, 102.97055]. *Type(s)*: holotype, MUMNH-UNI-0234. (MUMNH = Mahidol University Museum of Natural History).

Taxonomic opinions since Haas (1969a)

Contradens rolfbrandti – Konopleva *et al.* (2019*b*, p. 25), Jeratthitikul *et al.* (2019, p. 141, fig. 1.11–1.12), Bolotov *et al.* (2020, table S1).

Material examined

4 lots (Table S1).

Diagnosis

Morphologically very similar to *L. contradens* and *L. maenamensis* but tends to have a more elongate shell outline.

Distribution

Known from a few localities in the Mekong drainage near Vientiane, Laos (Fig. 13).

Ecoregion

Khorat Plateau.

Remarks

Lens rolfbrandti was previously thought to be restricted to its type locality (Jeratthitikul *et al.* 2019); recent field and museum sampling has expanded the known distribution of the species to include several localities in the northern part of the Khorat Plateau ecoregion (Fig. 13).

Lens semmelinki (von Martens, 1891), comb. nov.

(Table 1; Fig. 1, 11, 15; Table S1)

Unio semmelinki von Martens, 1891, p. 111 – figured in Haas 1914, p. 231, pl. 20, fig. 6–7. *Type locality*: 'Tana-laut insulae Borneo' [Tanah Laut, South Kalimantan Province, Borneo, Indonesia, -3.88333, 114.86667]. *Type(s)*: syntype, SMF 3604 (Zilch 1967, p. 92).

Taxonomic opinions since Haas (1969a)

Contradens semmelincki [sic] [in part] - Haas (1969a, p. 97).

Contradens semmelinki – Graf and Cummings (2007, p. 310), Zieritz *et al.* (2018*a*, online table 1), Do *et al.* (2018, p. 5), Konopleva *et al.* (2019*a*, table S2), Zieritz *et al.* (2020, p. 2237).

Material examined

3 lots (Table S1).

Diagnosis

Unknown.

Distribution

Coastal drainages of southern Borneo (Fig. 15).

Ecoregion

South-eastern Borneo.

Remarks

The validity of this species is uncertain, and it may be a synonym of *L. contradens*. The species has not yet been included in a molecular phylogeny.

Genus Physunio Simpson, 1900

Physunio Simpson, 1900: 830. *Type species: Unio gravidus* Lea, 1856 by original designation.

Diagnosis

This taxon can be distinguished from its sister taxon *Trapezoideus* by its generally larger and thinner shells. Species of *Physunio* tend to have a more circular (*P. superbus* and *P. massini*) or elongate (*P. modelli* and *P. pellucidus*) shell outline (Fig. 17), in comparison to the more rhomboidal or trapezoidal shape of *Trapezoideus*.

Distribution

From the Mae Klong drainage in the west to the Mekong drainage in the east. Also occurs in the Malay Peninsula and a few records from the islands of Sumatra and Java.

Species

We recognise four valid species in the genus Physunio (Fig. 17).

- Physunio superbus (Lea, 1843).
- Physunio massini (Morelet, 1864), stat. rev.
- Physunio modelli Brandt, 1974.
- Physunio pellucidus, sp. nov.

Remarks

Velunio Haas, 1919 has occasionally been considered a junior synonym or subgenus of *Physunio* (Modell 1964; Haas 1969*a*; Subba Rao 1989; Ramakrishna and Dey 2007) but its type species, *Unio velaris* Sowerby 1868, from 'Assam' does not resemble most Contradentini and more likely belongs to *Lamellidens* Simpson, 1900 (Parreysiinae: Lamellidentini). However, this point is mostly unnecessary because *Velunio* Haas, 1919 is not an available name because its type species *Unio velaris* Sowerby, 1868 is a misidentified reference to *Unio velaris* Hanley, 1856 and is therefore not available, and by extension neither is *Velunio* Haas, 1919.

There are two morphologically divergent clades within *Physunio* (Fig. 18): a clade of strongly inflated and circular mussels (*P. superbus* and *P. massini*) and a clade of much more compressed and elongate mussels (*P. modelli* and *P. pellucidus*).

Physunio superbus (Lea, 1843)

(Tables 1, 3; Fig. 1, 9, 10, 17–19; Tables S1, S2; Fig. S1–S5)

- *Unio superbus* Lea, 1843, p. [1] figured in Sowerby 1867, pl. 59, fig. 295. *Type locality*: 'New Holland' [Australia, dubious]. *Type(s)*: lectotype, USNM 83934 (Johnson 1974, p. 142, as the holotype).
- Unio gravidus Lea, 1856, p. 93 figured in Lea 1857, p. 292, pl. 24, fig. 5. Type locality: 'Siam' [Thailand, not fixed]. Type(s): lectotype, USNM 83935 (Johnson and Baker 1973, p. 157, as the holotype).



Fig. 17. Representative individuals of each Physunio species. Scale bar equals 1 inch (2.54 mm).



Fig. 18. COI gene tree of Physunio and Trapezoideus. Nodal support (UFBoot) is listed above branches.

- *Unio velaris* Hanley, 1856, p. 385, pl. 23, fig. 42. *Type locality*: Bugis, Celebes [Bugis, Sulawesi, not fixed]. *Type(s)*: unknown. *Remarks*: Attributed to 'Benson, MS'.
- Unio abnormis Morelet, 1862, p. 480. Type locality: Bangkok. [Chao Phraya drainage, Bangkok, Bangkok Metropolitan Administration, Thailand, 13.75398, 100.50144]. Type(s): syntype, NHMUK 1893.2.4.1394 (Johnson 1971, p. 78).

Taxonomic opinions since Haas (1969a)

Physunio (s.s.) superbus [in part] – Haas (1969a, p. 89).

Physunio (s.s.) gravidus - Haas (1969b, N428, fig. D28:5).

- Physunio superbus [in part] Brandt (1974, p. 294, pl. 25, fig. 57).
- Physunio superbus Marwoto (1987, p. 306), Graf and Cummings (2007,
 - p. 311), Bogan and Do (2014, p. 114), Pfeiffer and Graf (2015, p. 315),

Zieritz *et al.* (2016, p. 1071), Bolotov *et al.* (2017*a*, p. 12, table S1; 2017*b*, table S1), Zieritz *et al.* (2018*a*, online table 1), Razak *et al.* (2019, p. 459), Konopleva *et al.* (2019*a*, table S2; 2019*b*, p. 30), Huang *et al.* (2019, p. table S4), Pfeiffer *et al.* (2019, p. 116), Jeratthitikul *et al.* (2019, p. 136), Zieritz *et al.* (2020, p. 2243), Bolotov *et al.* (2020, table S1).

Material examined

97 lots (Table S1).

Diagnosis

Morphologically very similar to *P. massini* but tends to be less inflated and has a less prominent umbo sculpture.



Fig. 19. Dot distribution map of *Physunio superbus*, *P. massini*, *P. modelli s.l.* and *P. pellucidus*.

Distribution

Widespread in the Mae Klong, Chao Phraya, and Bang Pakong drainages in eastern and central Thailand, as well as the Malay Peninsula. Also known from Sumatra and Java (Fig. 19).

Ecoregions

Mae Klong, Malay Peninsula Eastern Slope, Southern Sumatra–Western Java, Chao Phraya.

Remarks

Haas (1969*a*) and Brandt (1974) considered *Unio macropterus* Dunker, 1846 a junior synonym of *P. superbus* but the type locality of that nominal species is from Brazil. We follow Simone (2006) and consider *Unio macropterus* Dunker, 1846 a junior synonym of *Prisodon obliquus* Schumacher, 1817. Despite occupying several geographically divergent drainages, all the sampled *P. superbus* individuals are molecularly very similar (Fig. 18). *Physunio superbus* is one of the two Contradentini species thought to occur in both mainland South-east Asia and the Malay Archipelago (the other being *L. contradens*). *Physunio superbus* populations on the Malay Archipelago are known from only a few records and while some specimens strongly resemble mainland South-east Asia populations (e.g. UMMZ 110123), others are much more strongly compressed and elongate (e.g. SMF 14736) and may represent an unrecognised species. Sampling putative *P. superbus* populations from the Malay Archipelago will be necessary to understanding its species boundaries and the historical freshwater connections between mainland south-east Asia and the Malay Archipelago.

Local common names for this species are loosely translated in English to 'rice soup mussel' or 'cow nose mussel' (Nabhitabhata 2009).

Physunio massini (Morelet, 1864), stat. rev.

(Table 1; Fig. 1, 17–19; Tables S1, S2)

Unio massini Morelet, 1864, p. 288 – figured in Morelet 1875, p. 348, pl. 15, fig. 2 [1]. *Type locality*: 'Cochinchina' [Vietnam, not fixed]. *Type(s)*: lectotype, NHMUK 1893.2.4.1590 (Johnson 1971, p. 88, as the holotype).

Taxonomic opinions since Haas (1969a)

Physunio (s.s.) superbus [in part] – Haas (1969*a*, p. 90). Physunio superbus [in part] – Brandt (1974, p. 294). Physunio superbus – Do *et al.* (2018, p. 10, table 2).

Material examined

19 lots (Table S1).

Diagnosis

Morphologically very similar to *P. superbus* but tends to be more inflated and has a more nodulous umbo sculpture.

Distribution

Mekong drainage in Cambodia (Fig. 19).

Ecoregion

Mekong Delta.

Remarks

Physunio massini is herein resurrected from synonymy to recognise that the Mekong populations previously identified as *P. superbus* represent a well supported and phylogenetically divergent lineage distinct from *P. superbus*. Unlike its sister species, *P. superbus*, which is geographically widespread, *P. massini* is known only from the Mekong Delta ecoregion (Fig. 19).

Physunio modelli Brandt, 1974

(Tables 1, 3; Fig. 1, 9, 17–19; Tables S1, S2; Fig. S1–S5)

Physunio modelli Brandt, 1974, p. 297, pl. 25, fig. 62. Type locality: 'Maenam Pong at Pong Nip Dam, Kon Kaen Province' [Pong River, Pong Nip Dam (=Nam Pong Dam), Khon Kaen Province, Thailand, 16.77345, 102.61938]. Type(s): holotype, SMF 220841 (Zilch 1983, p. 83).

Taxonomic opinions since Haas (1969a)

Physunio modelli [in part] – Brandt (1974, p. 297, pl. 25, fig. 62).

Physunio modelli – Graf and Cummings (2007, p. 311), Bolotov et al. (2017a, p. 9, table S1; 2017b, table S1), Lopes-Lima et al. (2017, p. 177), Zieritz et al. (2018a, online table 1), Do et al. (2018, p. 10, table 2), Bolotov et al. (2018, table S1), Konopleva et al. (2019a, table S2; 2019b, p. 30), Huang et al. (2019, table S4), Jeratthitikul et al. (2019, p. 136), Lopes-Lima et al. (2020, table 1), Bolotov et al. (2020, table S1), Zieritz et al. (2020, p. 2243).

Material examined

55 lots (Table S1).

Diagnosis

Morphologically very similar to its sister species, *P. pellucidus*, but tends to be taller and have a higher posterior wing. Very thin shell and delicate teeth in comparison to other Contradentini of its size.

Distribution

Mekong drainage in Thailand, Laos, and Cambodia. Primarily found in the Mun River watershed but also occurs in the Loei, Songkhram, Stung Treng, and Tonle Sap watersheds (Fig. 19).

Ecoregions

Lower Lancang, Khorat Plateau, Kratie-Stung Treng, Mekong Delta.

Remarks

We did not recover P. modelli as monophyletic (Fig. 18). Specimens from the Songkhram river (P. modelli 'Songkhram') were recovered in a divergent lineage that formed a polytomy with the P. modelli specimens from the Khorat Plateau, Kratie-Stung Treng, and Lower Lancang ecoregions, and P. pellucidus. A specimen from the Tonle sap (P. modelli 'Tonle Sap') represents a third lineage reluctantly assigned to P. modelli. Greater geographic and molecular character sampling is necessary to circumscribe the species boundaries in this clade. The distribution of the P. modelli clade (in the strictest sense) suggests that there has been an intradrainage stream-capture event; where the headwaters of the Mun watershed were captured by the Loei watershed (Fig. 19). This is unlike all the other hypothesised stream captures in that the faunal exchange occurred between two adjacent watersheds of the same drainage, and not between two watersheds of different drainages.

Physunio pellucidus, sp. nov.

(Tables 1, 3; Fig. 1, 9, 17–19; Tables S1, S2; Fig. S1–S5)

Type locality

Thuai River, Rt. 212 bridge S of Tha Uthen, Nakhon Phanom Province, Thailand, 17.56200, 104.60900.

Туре

Holotype, UF 564750. Paratype, UF 507799 (n = 2), same locality as the holotype.

Taxonomic opinions since Haas (1969a) Physunio modelli [in part] – Brandt (1974, p. 297).

Material examined

9 lots (Table S1).

Diagnosis

Morphologically very similar to its sister species, *P. modelli*, but tends to be narrower and have a less prominent posterior wing. Very thin shell and delicate teeth in comparison to other Contradentini of its size.

Description

Shell elongate, thin, translucent. Anterior end short, broadly rounded. Posterior end long, tapering, bluntly pointed. Dorsal margin straight. Ventral margin slightly curved to straight. Posterior ridge broadly rounded. Posterior slope steep, especially near umbo. Periostracum smooth, yellowish-brown, occasionally dull grey-green. Posterior slope often with two green rays. Umbo shallow. Nacre iridescent, very faintly purpleish-blue, translucent. Pseudocardinal and lateral teeth parallel, blade-like, delicate. Left valve with two lateral teeth, dorsal tooth much shorter than ventral. Left valve with one pseudocardinal, long, taller than laterals. Right valve, with one lateral tooth, long, straight. Left valve with two long pseudocardinal. Supra-anal aperture short. Pallial fusion between supra-anal and excurrent 3× times larger than supraanal aperture. Excurrent aperture smooth, equal in length to incurrent. Incurrent aperture with multiple rows of long simple papillae. Demibranch perforated. Interior demibranch attached to visceral mass only anteriorly. Ectobranchous brooding, marsupium laterally swollen, blush when glochidia are fully developed. Bilaterally asymmetrical glochidia.

Distribution

Mekong drainage in Thailand and Laos (Fig. 19).

Ecoregions

Lower Lancang, Khorat Plateau.

Remarks

This species is split out of *P. modelli* to recognise that there are two morphologically similar but well supported and phylogenetically divergent lineages occurring in the Khorat Plateau ecoregion of the Mekong drainage. Interestingly, this species is found primarily in or near the Mekong River proper and is largely absent from the Mekong's larger watersheds. The opposite pattern is true for its sister species, *P. modelli*, which is found primarily in the Mekong's larger watersheds and absent from the Mekong roper (Fig. 19).

Genus Pressidens Haas, 1910

Pressidens Haas, 1910: 102. Type species: Pressidens moellendorffi Haas, 1910 by original designation.

Diagnosis

Thick wrinkled umbo sculpture distinguishes this taxon from all other taxa in the Contradentini.

Distribution

The islands of Borneo, Banguey Island, and Palawan.

Species

We recognise one valid species in the genus Pressidens (Fig. 20).

• Pressidens exanthematicus (Küster, 1861)

Remarks

Like many of the freshwater mussels of the Malay Archipelago this hypothesised taxon is poorly understood. Its position among the Contradentini remains untested but it is similar to other members of the tribe in that it has a thin shell, delicate teeth, and a broadly rounded posterior slope (Fig. 20). However, the strongly wrinkled umbo is unlike most other members of the Contradentini. Resolving the systematic position of this taxon will be critical to a better understanding of freshwater mussel biogeography in South-east Asia.

Pressidens exanthematicus (Küster, 1861)

(Table 1; Fig. 1, 10, 20, 21; Table S1)

- *Unio exanthematicus* Küster, 1861, p. 243, pl. 81, fig. 2. *Type locality:* 'Ostindien' [Eastern India]. *Type(s):* unknown.
- Pseudodon insularis Drouët, 1894, p. 217, fig. 2. Type locality: 'L'ile Banguey, à l'extrémité Nord de Bornéo' [Banggi Island, Sabah State, Borneo, Indonesia, 7.28333, 117.20000]. Type(s): syntype, SMF 3602 (Zilch 1967, p. 88).
- Pressidens moellendorffi Haas, 1910, p. 103. Type locality: 'Palawan' [Palawan Island, Province of Palawan, Philippines, 9.52750, 118.39750]. Type(s): syntype, SMF 3600 (Zilch 1967, p. 88).

Taxonomic opinions since Haas (1969a)

- *Pressidens exanthematicus* Haas (1969*a*, p. 81), Graf and Cummings (2007, p. 311), Zieritz *et al.* (2018*b*, p. 131), Zieritz *et al.* (2018*a*, online table 1), Zieritz *et al.* (2020, p. 2238).
- *Pressidens insularis* Haas (1969*a*), Graf and Cummings (2007, p. 311), Zieritz *et al.* (2018*b*, p. 131), Zieritz *et al.* (2018*a*, online table 1), Zieritz *et al.* (2020, p. 2238).
- *Pressidens moellendorffi* Haas (1969*a*, p. 82; 1969*b*, N430, fig. D29:6), Graf and Cummings (2007, p. 311), Zieritz *et al.* (2018*a*, online table 1).

Material examined

27 lots (Table S1).

Diagnosis

Same as the genus.

Distribution

Known from the islands of Borneo, Banguey and Palawan (Fig. 21).

Ecoregions

North-eastern Borneo, North-western Borneo, and Palawan.



Fig. 20. Representative species of *Pressidens*, *Solenaia* and *Trapezoideus*. Scale bars equal 1 inch (2.54 mm). Image of *Trapezoideus lenya* reproduced from Bolotov *et al.* (2020) (approximately to scale).

Remarks

In the recent past this species has been treated as three distinct species: *P. exanthematicus* (Borneo), *P. insularis* (Borneo and Palawan), and *P. moellendorffi* (Palawan) (see taxonomic opinion section above). Rather than three species with partially overlapping ranges on three separate islands, we hypothesise that *Pressidens* is monotypic. While there is considerable morphological variation in the examined material, it does not appear to vary as a function of the three nominal species or the islands in which they are thought to occur. Given the available data, this conservative hypothesis of

a single *Pressidens* species seems more useful. The species has not yet been included in a molecular phylogeny.

Genus Solenaia Conrad, 1869

Solenaia Conrad, 1869: 249. Type species: Mycetopus emarginatus Lea, 1860 by monotypy.

Diagnosis

Solenaia can be distinguished from all other Contradentini by its ultra-elongate shell shape and the lack of dentition (at least in adults) (Fig. 10).



Fig. 21. Dot distribution map of *Pressidens exanthematicus* and *Rectidens sumatrensis*.

Distribution

Western and central Thailand.

Species

We recognise one species in the genus Solenaia (Fig. 20).

• Solenaia emarginata (Lea, 1860).

Remarks

Solenaia was previously thought to be a quite diverse and geographically widespread Asian genus (5 species, Graf and

Cummings 2007). The genus was recently hypothesised to be polyphyletic based on the presence of divergent larval morphologies between its putative species (bilaterally symmetrical and bilaterally asymmetrical glochidia) and a strongly disjunct reported range (India, Thailand, China) (Pfeiffer and Graf 2015). Recent molecular phylogenies have supported that hypothesis – recovering *Solenaia* species in three divergent clades of the Gonideinae (Lopes-Lima *et al.* 2017; Huang *et al.* 2019; Pfeiffer *et al.* 2019). Huang *et al.* (2019) partially revised *Solenaia sensu latu* by describing the new genus, *Parvasolenaia* Huang & Wu in Huang *et al.* (2019), that included Ρ. rivularis, P. triangularis and P. neotriangularis. However, Huang et al. (2019) suggested that the 'other' Chinese Solenaia (S. oleivora [=S. iridinea] and S. carinata) would be recovered in a clade with the type species of Solenaia, S. emarginata, from Thailand, However, that hypothesis is untenable because S. oleivora [=S. iridinea] and S. carinata belong to the Gonideini and have unhooked glochidia (Huang et al. 2013; Huang et al. 2019) while S. emarginata belongs to the Contradentini and has bilaterally asymmetrical glochidia (Deein et al. 2008; Pfeiffer and Graf 2015). As such, 'S.' oleivora (='S'. iridinea) and 'S.' carinata do not belong to Solenaia or the Contradentini and appear to belong to a separate, currently unrecognised genus in the tribe Gonideini.

A similar morphologically untenable hypothesis was recently proposed for the Indian taxa formally attributed to Solenaia. Balwantia Prashad, 1919 has been considered a junior synonym of Solenaia since Subba Rao (1989) but was recently recognised as a valid genus in the Contradentini and is thought to consist of three species -B. soleniformis, B. baniensis and B. elongatula (Bolotov et al. 2020). However, the type species of Balwantia, Anodonta soleniformis Benson, 1836, has unhooked glochidia (Prashad 1919, Pfeiffer and Graf 2015) and is very unlikely to belong to the Contradentini because that taxon is diagnosed by having bilaterally asymmetrical glochidia. Whereas, 'B.' baniensis, and 'B.' elongatula are clearly part of the Contradentini and closely related to Yaukthwa (Fig. 25) and those taxa are herein transferred to Yaukthwa. See remarks in the taxonomic account of Yaukthwa for further details regarding that hypothesis.

We recognise *Solenaia* as monotypic. The Chinese taxa recently attributed to *Solenaia* (i.e. '*S*.' *oleivora* [='*S*'. *iridinea*] and '*S*.' *carinata*) appear to belong to a currently unrecognised genus of the Gonideini, while the Indian species formally attributed to *Solenaia* ('*S*.' *soleniformis*) is likely to represent the genus *Balwantia* – whose systematic position remains largely unknown, but based on our understanding of synapomorphy is not part of Contradentini and may belong to the Parreysiinae (Pfeiffer and Graf 2015).

Solenaia emarginata (Lea, 1860)

(Tables 1, 3; Fig. 1, 9, 10, 12, 20, 22; Tables S1, S2; Fig. S1–S5)

- *Mycetopus emarginatus* Lea, 1860, p. 308. *Type locality*: 'Siam' [Thailand, not fixed]. *Type(s)*: holotype by monotypy, USNM 86787 (Johnson 1974, p. 52).
- Solenaia khwaenoiensis Panha & Deein in Deein et al. 2004, p. 53, fig. 2, 3a. *Type locality*: Khwae Noi River, Ban Ta Ngam, Wat Bot District, Phitsanulok Province, Thailand, 17.01353, 100.33598. *Type(s)*: holotype, PRDC 10001 (PRDC = Museum of Phitsanulok Inland Fisheries Research and Development Center).

Taxonomic opinions since Haas (1969a)

- *Solenaia emarginata* Haas (1969*a*, p. 125; 1969*b*, N435, fig. D32:2), Graf and Cummings (2007, p. 311), Pfeiffer and Graf (2015, p. 314), Zieritz *et al.* (2018*a*, online table 1).
- *Solenaia khwaenoiensis* Deein *et al.* (2004, p. 53, fig. 2–3), Graf and Cummings (2007, p. 312), Pfeiffer and Graf (2015, p. 314), Kongim *et al.* (2015, p. 103), Zieritz *et al.* (2018*a*, online table 1), Pfeiffer *et al.* (2019, p. 116).

Material examined 3 lots (Table S1).

Diagnosis

Same as for genus.

Distribution

Mae Klong and Chao Phraya drainages of western and central Thailand (Fig. 22).

Ecoregions

Mae Klong, Chao Phraya.

Remarks

We consider Solenaia khwaenoiensis Panha & Deein in Deein et al. (2004) a junior synonym of Mycetopus emarginatus Lea, 1860. The type locality of Mycetopus emarginatus Lea, 1860 is 'Siam' and is too vague to determine what drainage the holotype was collected from. Despite this ambiguity, Solenaia emarginata was recently thought to be restricted to only western Thailand because at least one Solenaia record was known from the Mae Klong drainage (Deein et al. 2004) and a recently discovered population in the adjacent Chao Phraya drainage was thought to represent a new species, Solenaia khwaenoiensis Panha & Deein in Deein et al. (2004). This suggests that Solenaia emarginata is endemic to the Mae Klong and Solenaia khwaenoiensis is endemic to the Chao Phraya. However, this biogeographic hypothesis is unlike any other in the Contradentini or Rectidentini, in that no member of either clade is known to be endemic to the Mae Klong. That is, the entire Contradentini +Rectidentini fauna in the Mae Klong drainage is shared with the adjacent Chao Phraya drainage. We consider Solenaia khwaenoiensis a junior synonym of Solenaia emarginata on the basis that there are very few morphological differences between the two nominal species and the overwhelming biogeographic evidence suggests that no members of the Contradentini+Rectidentini are endemic to the Mae Klong.

Genus Trapezoideus Simpson, 1900

Trapezoideus Simpson, 1900: 858. *Type species*: *Unio foliaceus* Gould, 1843 by original designation.

Diagnosis

Distinguished from its sister taxon *Physunio* by being smaller and having a more trapezoidal shell outline, as opposed to circular (*P. superbus* and *P. massini*) or elongate (*P. modelli* and *P. pellucidus*) (Fig. 10).

Distribution

Western, central, and south-eastern Thailand, and north-western Malay Peninsula in Myanmar.

Species

We recognise three valid species in the genus *Trapezoideus* (Fig. 20).

• Trapezoideus foliaceus (Gould, 1843).



Fig. 22. Dot distribution map of Solenaia emarginata, Trapezoideus foliaceus, T. lenya and T. subviridis.

- Trapezoideus lenya Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020.
- Trapezoideus subviridis, sp. nov.

Remarks

Trapezoideus is one of only two genera of the Contradentini +Rectidentini to occur in the Lower Salween ecoregion and the ecoregions to the east, the other genus being *Lens*. The supraspecific relationships in this genus are poorly supported in our *COI* gene tree (Fig. 18) and generating a more robust phylogeny of the group will be necessary to understanding the biogeographic history of this clade, including its dispersal across the influential drainage divides between the Salween Province and the Thai Gulf Province (Fig. 7).

Trapezoideus foliaceus (Gould, 1843)

(Tables 1, 3; Fig. 1, 9, 10, 20, 22; Tables S1, S2; Fig. S1–S5)

Unio foliaceus Gould, 1843, p. 141. Type locality: 'Tavoy, Burmah' [Dawei, Tanintharyi Region, Myanmar, 14.07375, 98.19423]. Type(s): lectotype, USNM 84161 (Johnson 1964, p. 78).
Taxonomic opinions since Haas (1969a)

Trapezoideus foliaceus [in part] – Haas (1969a, p. 75).

- *Trapezoideus foliaceus* Haas (1969b, N435, fig. D32:9), Bolotov *et al.* (2017b, p. 10, table 3), Konopleva *et al.* (2019a, p. 4, fig. 2a–b, table S2; 2019b, p. 30), Pfeiffer *et al.* (2019, p. 116), Zieritz *et al.* (2020, p. 2243), Bolotov *et al.* (2020, p. 6, tables 3, S1).
- *Trapezoideus exolescens exolescens* [in part] Brandt (1974, p. 299), Subba Rao (1989, p. 195, fig. 432–433, 552–553), Ramakrishna and Dey (2007, p. 328).
- *Trapezoideus exolescens* [in part] Graf and Cummings (2007, p. 312), He and Zhuang (2013, p. 121).

Material examined

43 lots (Table S1).

Diagnosis

Conchologically very similar to *T. subviridus* but often has a less green posterior slope.

Distribution

Mae Klong and Chao Phraya drainages in western and central Thailand (Fig. 22).

Ecoregions

Mae Klong, Chao Phraya.

Remarks

The type locality of *Unio foliaceus* Gould, 1843 is 'Tavoy, Burmah' but the accuracy of this locality has been questioned (Konopleva *et al.* 2017, 2019*a*). The exact locality is never explicitly stated in the description but has been assumed as such because the specimens were sent to Augustus A. Gould by Rev. Francis Mason, a missionary living in Tavoy. Specimens morphologically similar to the type of *Unio foliaceus* are common and widespread in the upper reaches of Mae Klong drainage, which are very near the headwaters of the adjacent Tavoy drainage (Lower & Middle Salween ecoregion) (Fig. 22). It remains unclear whether the species occurs in the Tavoy drainage and is conspecific with populations in the Mae Klong and Chao Phraya, or the type locality is dubious; further sampling of the Tavoy drainage is needed.

Trapezoideus lenya Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020

(Table 1; Fig. 1, 20, 22; Table S1)

Trapezoideus lenya Bolotov *et al.*, 2020, p. 7, fig. 2E. *Type locality*: Lenya River Basin, 14 Mile Stream, Bokpyin, Taninthayi Division, Myanmar, 11.35083, 99.10934. *Type(s)*: holotype, RMBH biv0629_2.

Taxonomic opinions since Haas (1969a)

Trapezoideus lenya - Bolotov et al. (2020, p. 7, fig. 2E, tables 3, S1).

Material examined

1 lot (Tables S1-S2, Fig. S1-S5).

Diagnosis

Distinguished from *T. foliaceus* and *T. subviridis* by having a narrower anterior and wider posterior.

Distribution

Known only from the type locality in the Lenya River, northwestern Malay Peninsula in Myanmar (Fig. 22).

Ecoregion

Lower and Middle Salween.

Remarks

Trapezoideus lenya is the only species of the Contradentini +Rectidentini that has a distribution that is thought to terminate near the Isthmus of Kra, although the species is known only from its type locality so little can be said about its geographic scope. The Isthmus of Kra region, and more specifically the Tanintharyi–Lenya drainage divide, has recently been shown to be a significant biogeographic barrier for freshwater mussels (Bolotov *et al.* 2020), but its importance to the distribution and diversity of the Contradentini+Rectidentini appears to be limited.

Trapezoideus subviridis, sp. nov.

(Tables 1, 3; Fig. 1, 9, 20, 22; Tables S1, S2; Fig. S1–S5)

Type locality

Patong River, downstream of Khao Soi Dao Wildlife Sanctuary, Soi Dao District, Chanthaburi Province, Thailand, 13.10511, 102.19388.

Types

Holotype, UF 564751. Paratypes, UF 507543 (n = 8), same locality as the holotype.

Material examined

5 lots (Table S1).

Diagnosis

Conchologically very similar to *T. foliaceus* but often has a greener posterior slope.

Description

Shell trapezoidal, very thin, compressed. Anterior end narrow, broadly rounded. Posterior end squarish to rounded with moderate wing. Dorsal and ventral margins straight. Posterior ridge broadly rounded to biangulate, often with two green rays. Periostracum yellowish-brown, often with green posterior. Umbo shallow. Nacre iridescent, faintly purplish-blue, translucent, orangish in umbo. Pseudocardinal and lateral teeth nearly parallel, blade-like. Left valve with two lateral teeth, slightly curved, diverging. Left valve with one pseudocardinal, long, blade-like, more rounded near umbo. Right valve with one lateral tooth, long, slightly curved. Right valve with two pseudocardinal teeth, dorsal much smaller, occasionally reduced to swelling. Supra-anal aperture short. Pallial fusion between supra-anal and excurrent $2 \times$ longer than supra-anal aperture. Excurrent aperture smooth, slightly smaller than incurrent. Incurrent aperture with multiple rows of simple papillae. Demibranch perforated. Interior demibranch attached to visceral only anteriorly. Ectobranchous brooding, marsupium with moderate lateral inflation with unripe glochidia.

Distribution

Bang Pakong and Chantaburi drainages of south-eastern Thailand (Fig. 22).

Ecoregions:

Chao Phraya, Eastern Gulf of Thailand.

Remarks

Only species of the Contradentini+Rectidentini endemic to the coastal rivers of South-east Thailand.

Genus **Yaukthwa** Konopleva, Pfeiffer, Vikhrev, Kondakov, Gofarov, Aksenova, Lunn, Chan & Bolotov, 2019

Yaukthwa Konopleva et al., 2019. Type species: Trapezoideus nesemanni Konopleva, Vikhrev, Bolotov in Bolotov et al., 2017 by original designation.

Diagnosis

Distinguished from morphologically similar genera of *Lens* and *Trapezoideus* by its more rectangular shape, including a wider anterior and straighter ventral margin (Fig. 10).

Distribution

Widespread in Myanmar, known from one locality in northwestern Thailand.

Species

We recognise 11 valid species in the genus Yaukthwa (Fig. 23).

- Yaukthwa nesemanni (Konopleva, Vikhrev & Bolotov in Bolotov et al. 2017b).
- *Yaukthwa avaensis* Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020.
- Yaukthwa baniensis (Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020), comb. nov.
- Yaukthwa dalliana (Frierson, 1913).
- Yaukthwa elongatula Bolotov, Konopleva, Vikhrev, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Gofarov, Tomilova & Kondakov, 2019, comb. res.
- Yaukthwa inlenensis Konopleva, Pfeiffer, Vikhrev, Kondakov, Gofarov, Aksenova, Lunn, Chan & Bolotov, 2019.
- Yaukthwa paiensis Konopleva, Pfeiffer, Vikhrev, Kondakov, Gofarov, Aksenova, Lunn, Chan & Bolotov, 2019.
- *Yaukthwa panhai* (Konopleva, Bolotov & Kondakov in Bolotov *et al.* 2017*b*).
- Yaukthwa peguensis (Anthony, 1865).

- Yaukthwa rectangularis (Tapparone-Canefri, 1889), comb. nov.
- Yaukthwa zayleymanensis (Preston, 1912).

Remarks

Recent studies have substantially increased our phylogenetic understanding of this clade, including the description of the genus and seven new species (Bolotov et al. 2017b, 2019b, 2020; Konopleva et al. 2019a). Despite being quite speciesrich, the genus is apparently restricted to a narrow geographic range (Fig. 24). The genus is also known from relatively few records (Fig. 1) and six of the 11 species are known only from their type localities. Three of the five Yaukthwa species described before 2017 have not been included in a molecular phylogenetic analysis (Y)peguensis. Y. rectangularis and Y. zayleymanensis). These three species are the only Contradentini+Rectidentini species from Indochina not yet included in a molecular phylogeny (Fig. 25). Including representatives of these older named species in a phylogenetic analysis will be important to better understanding the systematics, species diversity, and biogeographic history of this clade.

The genus *Balwantia* was recently resurrected from synonymy under Solenaia for a clade hypothesised to contain Anodonta soleniformis Benson, 1836 (type species of Balwantia), Yaukthwa elongatula Bolotov, Konopleva, Vikhrev, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Gofarov, Tomilova & Kondakov, 2019, and Balwantia baniensis Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020 (Bolotov et al. 2020). Balwantia elongatula and B. baniensis are clearly part of Contradentini and were recovered as sister to Yuakthwa (Bolotov et al. 2020). However, the type species of Balwantia, Anodonta soleniformis Benson, 1836, has not been included in a phylogenetic analysis but based on our understanding of synapomorphy in freshwater mussels that species is distantly related to any member of the Contradentini including 'B.' elongatula and 'B.' baniensis. Bilaterally asymmetrical glochidia is an unambiguous synapomorphy of the Contradentini and Balwanatia solenifomis has unhooked glochidia (Prashad 1919; Pfeiffer and Graf 2015) and thus Balwantia sensu Bolotov et al. (2020) is unlikely to be monophyletic.

As such, we transfer Balwantia elongatula (Bolotov, Konopleva, Vikhrev, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Gofarov, Tomilova & Kondakov, 2019) back to its originally described position, Yaukthwa elongatula Bolotov, Konopleva, Vikhrev, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Gofarov, Tomilova & Kondakov, 2019, comb. res., and move Balwantia baniensis Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020 to Yuakthwa baniensis (Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020), comb. nov. We recognise *Balwantia* as a valid monotypic genus whose subfamily-level position remains untested but, given its larval morphology and distribution, it may be a member of the Parreysiinae (Pfeiffer and Graf 2015).

Yaukthwa nesemanni (Konopleva, Vikhrev & Bolotov in Bolotov *et al.* 2017*b*)

(Table 1; Fig. 1, 23–25; Table S1)

Trapezoideus nesemanni Konopleva, Vikhrev, Bolotov in Bolotov et al., 2017, p. 13, fig. 4c. Type locality: Tauk Ue Kupt River (Sittaung Drainage), Myanmar, 19.3074, 96.7219. Type(s): holotype, NCSM 103033. Remarks: Holotype transferred from RMBH biv255_2 in Konopleva et al. (2019a).

Taxonomic opinions since Haas (1969a)

Contradens sp. 3 - Bolotov et al. (2017a, table S1).

- *Trapezoideus nesemanni* Bolotov *et al.* (2017*b*, p. 10, 13, fig. 4c, tables 3, S1), Bolotov *et al.* (2018, table S1), Huang *et al.* (2019, table S4), Lopes-Lima *et al.* (2020, table 1).
- *Yaukthwa nesemanni* Konopleva *et al.* (2019*a*, p. 7, table S1; 2019*b*, p. 30), Bolotov *et al.* (2019*a*, p. 2, table S1), Bolotov *et al.* (2020, tables 3, S1), Zieritz *et al.* (2020, p. 2243).

Material examined

1 lot (Table S1).

Diagnosis

Similar to *Y. panhai* but differs by its thinner shell and shallow adductor muscle scars (Bolotov *et al.* 2017*b*).

Distribution

Known only from the type locality in the Sittaung drainage, south-central Myanmar (Fig. 24).

Ecoregion

Sittaung-Irrawaddy.

Yaukthwa avaensis Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020

(Table 1; Fig. 1, 23–25; Table S1)

Yaukthwa avaensis Bolotov et al., 2020, p. 8, fig. 2F. Type locality: Tarkat Stream (Irrawaddy Drainage), Kachin State, Myanmar, 25.27580, 97.27220. Type(s): holotype, RMBH biv0680_3.

Taxonomic opinions since Haas (1969a)

Yaukthwa avaensis - Bolotov et al. (2020, p. 8, fig. 2F, tables 3, S1).

Material examined

1 lot (Table S1).

Diagnosis

Distinguished from other *Yaukthwa* by its more ovate shell outline and more pointed posterior (Bolotov *et al.* 2020).

Distribution

Known only from the type locality in the Irrawaddy drainage, northern Myanmar (Fig. 24).

Ecoregion

Sittaung-Irrawaddy.

Yaukthwa baniensis (Bolotov, Konopleva, Vikhrev, Gofarov, Lopes-Lima, Bogan, Lunn,

Chan, Win, Aksenova, Tomilova, Tanmuangpak, Tumpeesuwan & Kondakov, 2020), comb. nov.

(Table 1; Fig. 1, 23-25; Table S1)

Balwantia baniensis Bolotov *et al.* 2020, p. 8, fig. 2C. *Type locality:* Bani River (Irrawaddy Drainage), near Bangong village, Magway District, Myanmar, 19.32470, 94.98390. *Type(s):* holotype, RMBH biv0666_2.

Taxonomic opinions since Haas (1969a)

Balwantia baniensis – Bolotov et al. (2020, p. 5, fig. 2C, tables 3, S1). Balwantia myanmarensis – Bolotov et al. (2020, SI 1).

Material examined

1 lot (Table S1).

Diagnosis

Yaukthwa baniensis is distinguished from all other members of *Yaukthwa*, except its sister species *Y. elongatula*, by its strongly reduced dentition. It is thought to be distinguished from *Y. elongatula* by having a more rostrate anterior margin, a more inflated shell, and bars on the posterior slope (Bolotov *et al.* 2020).

Distribution

Known only from the type locality in the Irrawaddy drainage, southern Myanmar (Fig. 24).

Ecoregion

Sittaung–Irrawaddy.

Remarks

This species is herein transferred from *Balwantia* to *Yaukthwa* based on the divergent larval morphologies between *Balwantia* and members of the Contradentini (Pfeiffer and Graf 2015).

Yaukthwa dalliana (Frierson, 1913)

(Table 1; Fig. 1, 23–25; Table S1)

Parreysia dalliana Frierson, 1913, p. 142 – figured in Haas 1919, pl. 32, fig. 4. Type locality: 'Birma' [Irawaddy basin, Lashio, Shan State, Myanmar, 22.99483, 97.76528 (according to label data with the type)]. Type(s): lectotype, SMF 13699b (Johnson 1972, p. 143, as the holotype).

Taxonomic opinions since Haas (1969a)

Trapezoideus foliaceus [in part] – Haas (1969a, p. 76).

Trapezoideus exolescens [in part] – He and Zhuang (2013, p. 121).

Yaukthwa dalliana – Konopleva *et al.* (2019*a*, p. 7, table S1; 2019*b*, p. 30), Bolotov *et al.* (2019*b*, p. 2, table S1), Bolotov *et al.* (2020, tables 3, S1), Zieritz *et al.* (2020, p. 2243).

Material examined

6 lots (Table S1).



Fig. 23. Representative species of *Yaukthwa*. All RMBH and MSNG specimen images reproduced from Konopleva *et al.* (2017, 2019*a*) and Bolotov *et al.* (2020).

Diagnosis

Yaukthwa dalliana has much more robust teeth in comparison to other representatives of the genus.

Distribution

Irrawaddy drainage in northern Myanmar (Fig. 24).

Ecoregion Sittaung–Irrawaddy.

Remarks

There is considerable morphological variation in this putative species. Several records, including the lectotype, are morphologically divergent (robust lateral and pseudocardinal teeth, strongly sculptured umbo) and geographically distant from barcoded records (Fig. 24). As suggested by Konopleva *et al.* (2019*a*), including specimens from near the type locality will be important to better understanding the species' boundaries of this taxon.



Fig. 24. Dot distribution map of *Yaukthwa avaensis*, *Y. baniensis*, *Y. dalliana*, *Y. elongatula*, *Y. inlenensis*, *Y. nessemanni*, *Y. paiensis*, Y. *panhai*, *Y. peguensis*, *Y. rectangularis* and *Y. zaleymanensis*.

Yaukthwa elongatula Bolotov, Konopleva, Vikhrev, Lopes-Lima, Bogan, Lunn, Chan, Win, Aksenova, Gofarov, Tomilova & Kondakov, 2019, comb. res.

(Table 1; Fig. 1, 23–25; Table S1)

Yaukthwa elongatula Bolotov et al. 2019, p. 9, fig. 5D. Type locality: Chindwin River, near Kalewa, Sagaing Region, Myanmar, 23.19180, 94.32170. Type(s): holotype, RMBH biv346_2. Taxonomic opinions since Haas (1969a)

Yaukthwa elongatula – Bolotov et al. (2019b, p. 9, fig. 5D), Konopleva et al. (2019b, p. 30).

Balwantia elongatula – Bolotov et al. (2020, tables 3, S1).

Material examined

9 lots (Table S1).



Fig. 25. COI gene tree of Yaukthwa. Nodal support (UFBoot) is listed above branches.

Diagnosis

Yaukthwa elongatula is distinguished from all other members of *Yaukthwa*, except its sister species *Y. baniensis*, by its strongly reduced dentition. It is thought to be distinguished from *Y. baniensis* by having a less rostrate anterior margin, a less inflated shell, and the absence of bars on the posterior slope (Bolotov *et al.* 2020).

Distribution

Irrawaddy drainage in western and central Myanmar (Fig. 24).

Ecoregion

Sittaung-Irrawaddy.

Remarks

Some specimens identified here as *Y. elongatula*, including one collected very near the type locality (FMNH 120070), look more similar to the holotype of *Y. baniensis* than the holotype of *Y. elongatula*. The fact that these species are relatively thin-

shelled and are often deeply buried in the substrate (Bolotov *et al.* 2020) may create a great deal of non-heritable variation in shell shape and is likely contributing to difficulties identifying historical specimens and delimiting species' geographic boundaries.

Yaukthwa inlenensis Konopleva, Pfeiffer, Vikhrev, Kondakov, Gofarov, Aksenova, Lunn, Chan & Bolotov, 2019

(Table 1; Fig. 1, 23–25; Table S1)

Yaukthwa inlenensis Konopleva et al., 2019, p. 10, fig. 4c. Type locality: Mway Stream (Salween Drainage), a tributary of Nam Pilu River, Shan State, Myanmar, 19.72660, 97.09920. Type(s): holotype, RMBH biv139_18.

Taxonomic opinions since Haas (1969a)

Contradens sp. 5 – Bolotov et al. (2017a, table S1).

Trapezoideus sp. 'Salween' – Bolotov *et al.* (2017*b*, p. 10, table 2), Bolotov *et al.* (2018, table S1).

Yaukthwa inlenensis – Konopleva et al. (2019a, p. 10, fig. 2, 4c; 2019b, p. 30), Bolotov et al. (2019b, p. 2, table S1), Bolotov et al. (2020, tables 3, S1), Zieritz et al. (2020, p. 2243).

Material examined

1 lot (Table S1).

Diagnosis

Yaukthwa inlenensis is morphologically very similar to *Y. paiensis* but has a larger and more sculptured umbo (Konopleva *et al.* 2019*a*).

Distribution

Inle and Moebyel lakes (Salween drainage) in eastern Myanmar (Fig. 24).

Ecoregion

Lower and Middle Salween (including Inle Lake).

Yaukthwa paiensis Konopleva, Pfeiffer, Vikhrev, Kondakov, Gofarov, Aksenova, Lunn, Chan & Bolotov, 2019

(Tables 1, 3; Fig. 1, 9, 10, 18, 23–25; Tables S1, S2; Fig. S1–S5)

Yaukthwa paiensis Konopleva et al., 2019, p. 9, fig. 4d. Type locality: Khong River (Salween Drainage), tributary of Pai River, off Rt. 1095, Pai District, Mae Hong Son Province, Thailand, 19.42460, 98.40130. Type(s): holotype, UF 505164.

Taxonomic opinions since Haas (1969a)

Yaukthwa paiensis – Konopleva *et al.* (2019*a*, p. 9, fig. 4d; 2019*b*, p. 30), Pfeiffer *et al.* (2019, p. 116), Bolotov *et al.* (2020, tables 3, S1), Zieritz *et al.* (2020, p. 2243).

Material examined

2 lots (Table S1).

Diagnosis

Yaukthwa paiensis is morphologically very similar to *Y. inlenensis* but has less prominent and sculptured umbo (Konopleva *et al.* 2019*a*).

Distribution

Known only from the type locality in the Salween drainage, north-western Thailand (Fig. 24).

Ecoregion

Lower and Middle Salween.

Remarks

Only Yaukthwa species known from Thailand.

Yaukthwa panhai (Konopleva, Bolotov & Kondakov in Bolotov *et al.* 2017*b*)

(Table 1; Fig. 1, 23–25; Table S1)

Trapezoideus panhai Konopleva, Bolotov & Kondakov in Bolotov et al., 2017, p. 13, fig. 4d. Type locality: Kyan Hone River (Sittaung

Drainage), Myanmar, 19.5059, 96.8280. *Type(s)*: holotype, NCSM 103036. *Remarks*: Holotype transferred from RMBH biv_138_4 in Konopleva *et al.* (2019*a*).

Taxonomic opinions since Haas (1969a)

Contradens sp. 4 – Bolotov et al. (2017a, table S1).

- *Trapezoideus panhai* Bolotov *et al.* (2017*b*, pp. 10, 13, fig. 4d, tables 3, S1), Bolotov *et al.* (2018, table S1), Huang *et al.* (2019, table S4).
- *Yaukthwa panhai* Konopleva *et al.* (2019*a*, p. 7, table S1; 2019*b*, p. 30), Bolotov *et al.* (2019*b*, p. 2, table S1), Bolotov *et al.* (2020, tables 3, S1).

Material examined

1 lot (Table S1).

Diagnosis

Yaukthwa panhai is morphologically very similar to *T. nesemanni* but has a thicker shell and more developed hinge and umbo (Bolotov *et al.* 2017*b*).

Distribution

Known only from the type locality in the Sittaung drainage, eastern Myanmar (Fig. 24).

Ecoregion

Sittaung-Irrawaddy.

Yaukthwa peguensis (Anthony, 1865)

(Table 1; Fig. 1, 23, 24; Table S1)

Unio peguensis Anthony 1865, p. 351, pl. 25, fig. 2. *Type locality*: 'Pegu, British Burma' [Pegu [=Bago], Bago Region, Myanmar, 17.33333, 96.48333]. *Type(s)*: lectotype, MCZ 161875 (Johnson 1956, p. 128, as the holotype). *Remarks*: Johnson (1956) gave MCZ 161876 as the catalogue number for both the holotype of *Anodon inornata* Anthony, 1866 and a paratype *Unio peguensis* Anthony, 1865.

Taxonomic opinions since Haas (1969a)

Trapezoideus foliaceus [in part] – Haas (1969a, p. 76).
Trapezoideus exolescens exolescens [in part] – Brandt (1974, p. 299).
Trapezoideus exolescens [in part] – He and Zhuang (2013, p. 121).
Trapezoideus peguensis – Bolotov et al. (2017b, p. 10, Table 3).
Yaukthwa peguensis – Konopleva et al. (2019a, p. 9), Bolotov et al. (2020, table 3).

Material examined

12 lots (Table S1).

Diagnosis

Yaukthwa peguensis is distinguished from other members of the genus by being more trapezoidal and laterally compressed.

Distribution

Irrawaddy drainage in southern Myanmar (Fig. 24).

Ecoregion

Sittaung-Irrawaddy.

Remarks

The species has not yet been included in a molecular phylogeny.

Yaukthwa rectangularis (Tapparone-Canefri, 1889), comb. nov.

(Table 1; Fig. 1, 23, 24; Table S1)

Unio rectangularis Tapparone-Canefri, 1889, p. 354. *Type locality*: 'Teinzo, nel fiume Mule, Monti E. di Bhamo.' [Moolay River [=Mole Chuang] (Irawaddy Drainage), Teinthaw Village, hills E Bhamo, Kachin State, Myanmar, 24.39780, 97.25190]. *Type(s)*: holotype, MSNG ?

Taxonomic opinions since Haas (1969a)

Indonaia rectangularis - Bolotov et al. (2019a, p. 25, fig. 1a-f).

Material examined

1 lot (Table S1).

Diagnosis

Closely resembles other members of the genus, especially *Y. paiensis*, but is less elongate and more laterally compressed.

Distribution

Known only from the type locality in the Irrawaddy drainage, northern Myanmar (Fig. 24).

Ecoregion

Sittaung-Irrawaddy.

Remarks

This species was recently hypothesised to be a member of the genus *Indonaia* (Parreysiinae: Indochinellini) based on shell shape, elevated umbo and dentition (Bolotov *et al.* 2019*b*). However, this species shares several traits that are common among the Contradentini, and especially the genus *Yaukthwa*, including a rectangular shell outline, smooth yellow periostracum, oblique green ridges on the posterior slope, and wrinkles on the posterior slope that are largely perpendicular to the shell margin. The wrinkles on the posterior slope described as 'a unique feature' and 'never seen in other species' by Bolotov *et al.* (2019*b*) is a common trait in many members of the Contradentini including *Yaukthwa* (see fig. 4 in Konopleva *et al.* 2019*a*; Fig. 23). As such, we hypothesise that this species belongs to the genus *Yaukthwa*. The species has not yet been included in a molecular phylogeny.

Yaukthwa zayleymanensis (Preston, 1912)

(Table 1; Fig. 1, 23, 24; Table S1)

Trapezoideus foliaceus var. zaleymanensis, Preston 1912, p. 307.
Type locality: 'Bhamo' [Bhamo, Kachin State, Myanmar, 24.25639, 97.21967]. Type(s): syntype, SMF 3615 (Zilch 1967, p. 87). Remarks: Attributed to 'Neville MS'. Preston stated that the 'type' was from Bhamo. The syntype referenced above is from 'Zayleman'.

Taxonomic opinions since Haas (1969a)

Trapezoideus misellus [in part] - Haas (1969a, p. 76).

Trapezoideus exolescens exolescens [in part] – Brandt (1974, p. 299), Subba Rao (1989, p. 195), Ramakrishna and Dey (2007, p. 328).
Trapezoideus exolescens [in part] – He and Zhuang (2013, p. 121).
Trapezoideus subclathratus – Bolotov et al. (2017b, p. 10).
Yaukthwa zayleymanensis – Konopleva et al. (2019a, p. 8), Bolotov et al. (2020, tables 3, S1).

Material examined

8 lots (Table S1).

Diagnosis

Yaukthwa zayleymanensis is distinguished from other members of the genus by being more delicate and more dorso-ventrally narrow.

Distribution

Irrawaddy drainage in central and northern Myanmar (Fig. 24).

Ecoregion

Sittaung-Irrawaddy.

Remarks

The species has not yet been included in a molecular phylogeny.

RECTIDENTINI Modell, 1942

Type: Rectidens Simpson, 1900.

Diagnosis

The Rectidentini is distinguished from its sister group the Contradentini by having bilaterally symmetrical glochidia. Conchologically, the Rectidentini are more elongate and have a bluntly pointed posterior end in comparison to the Contradentini, which are generally more circular or rectangular and have a more broadly rounded posterior. The Rectidentini also tend to have a sharper posterior ridge and a shorter posterior slope (excluding the wing of *Hyriopsis*) than the Contradentini (Fig. 10).

Distribution

Widespread in Indochina from the Mae Klong in the west and to the Mekong drainage in the east. Also occurs on the Malay Peninsula and the islands of Sumatra, Java and Borneo.

Genera

We recognise six genera in the Rectidentini (Fig. 10).

- Rectidens Simpson, 1900.
- Ctenodesma Simpson, 1900.
- Elongaria Haas, 1911.
- Ensidens Frierson, 1911.
- Hyriopsis Conrad, 1853.
- Prohyriopsis Haas, 1914.

Remarks

The position of *Elongaria* and *Prohyriopsis* among the Rectidentini remains untested. However, the type species of *Prohyriopsis* is morphologically very similar to *Hyriopsis*,

and the type species *Elongaria* is morphologically very similar to *Rectidens*, so their positions among the Rectidentini seem likely. The systematic position of *?Elongaria trompi* among the Rectidentini is much more tenuous (Pfeiffer *et al.* 2018*a*) and is further described in the taxonomic account for that species.

Key to the genera of the Rectidentini

The practicality of this key is complicated by the fact that several of these genera may not be valid or monophyletic (e.g. *Elongaria*, *Ctenodesma*).

- 1. Wing present
 2.

 Wing absent
 3.

 2. Wing large, sculpturing absent
 Hyriopsis.
- Wing small, sculpturing present
 Prohyriopsis.

 3. Steep posterior slope, dorsal margin longer than ventral
 Ensidens.

- *?*Elongaria trompi* also has sculpture but that species may not belong to the Rectidentini see remarks in the species account.

Genus Rectidens Simpson, 1900

Rectidens Simpson, 1900: 853. *Type species: Unio prolongatus* Drouët, 1894 by original designation.

Diagnosis

Rectidens is the most elongate genus of the Rectidentini. *Rectidens* is morphologically very similar to *Elongaria orientalis* but tends to have a sharper posterior ridge and is often more biangulate (Fig. 26). *Rectidens* also tends to have a darker periostracum (brown to black) in comparison to *E. orientalis* (greenish-yellow to brown). *Rectidens* can be distinguished from *Ctenodesma borneensis* by its larger size and smoother shell disc.

Distribution

Malay Peninsula, and the islands of Sumatra, Java and Borneo.

Species

We recognise one valid species in the genus Rectidens (Fig. 26).

• Rectidens sumatrensis (Dunker, 1852)

Remarks

Distinguishing *Rectidens sumatrensis* from *Elongaria orientalis* using shell characters is difficult or impossible. Affandi *et al.* (2017) suggested the two species can be distinguished by the presence of wrinkles ventral to the pallial line in *Rectidens*. However, only one *Rectidens* specimen was included in their molecular assessment and the sequence data referenced in the paper remains unavailable at the time of this publication. Furthermore, the presence of wrinkles ventral to the pallial line is not unique to *Rectidens* and are quite common in many Rectidentini.

Rectidens sumatrensis (Dunker, 1852)

(Tables 1, 3; Fig. 1, 9, 10, 21, 26, 27; Tables S1, S2; Fig. S1–S5)

Unio sumatrensis Dunker, 1852 (non Lea, 1859), p. 52 – figured in Haas 1914, p. 230, pl. 28, fig. 3–6. Type locality: 'Ins. Sumatra (Dana

- Unio perakensis De Morgan, 1885 (non Preston, 1912), p. 424, pl. 9, fig. 3–4.
 Type locality: 'S. Kinta (Pérak)' [Kinta River (Perak Drainage), Kinta District, Perak State, Malaysia, 4.50448, 101.05479].
 Type(s): unknown.
- Unio lingulatus Drouët & Chaper, 1892, p. 149, pl. 5, fig. 7–9. Type locality: 'Sebroeang, à Bornéo' [Soengai Sebroeang (Kapus Drainage), Sebroeang, West Kalimantan Province, Borneo, Indonesia, 0.43333, 111.88333]. Type(s): syntype, MNHN-IM-2000–1737.
- Unio prolongatus Drouët, 1894 (non Fischer & Crosse, 1894), p. 216, fig. 1. Type localities: 'Le Niah, Riviere du nord de Borneo.' [Sungai Niah, Sarawak Province, Borneo, Malaysia, 3.86841, 113.73211. Type(s): unknown. Remarks: Primary homonym of Unio calamitarum var. B prolongata Fischer & Crosse, 1894: 613.
- Microcondylaea gracilis Strubell, 1897, p. 8 figured in Haas 1914, p. 230, pl. 27, fig. 6–7; pl. 28, fig. 1–2. *Type locality*: 'Südsumatra' [South Sumatra, Indonesia]. *Type(s)*: syntype, SMF 3610 (Zilch 1967, p. 90).
- Unio palembangensis Strubell, 1897, p. 10. Type locality: 'Südsumatra' [South Sumatra, Indonesia]. Type(s): syntype, SMF 3611 (Zilch 1967, p. 90).
- Unio pahangensis E.A. Smith, 1899, p. 315, text figure. *Type locality*: 'Pahang River, Malay Peninsula' [Pahang River, Pahang Sultanate, Malaysia, 3.53333,103.46667]. *Type(s)*: holotype by monotypy, NHMUK 1899.9.4.1 (Johnson 1971, p. 90).
- Unio palembangensis pahumbaensis von Martens, 1900, p. 14 figured in Haas 1914, p. 230, pl. 28, fig. 2, as pahoembaensis. Type locality: 'Pahumba, N. Sumatra' [Pahumba, Northern Sumatra, Indonesia, not fixed]. Type(s): syntype, SMF 3612 (Zilch 1967, p. 90).
- Unio pressirostris von Martens, 1900, p. 14 figured in Haas 1914, p. 226, pl. 27, fig. 1–3. *Type locality*: 'See Danau Baru, Indragiri, Sumatra' [Indragiri River, Danau Baru, Riau Province, Sumatra, Indonesia, -0.33196, 102.40482]. *Type(s)*: syntypes, SMF 168269 (Zilch 1967, p. 90) (n=6.5); NHMUK 1901.6.14.4 (n=1) (Johnson 1971, p. 91, as a paratype); ZMB 51794 (n = 1).
- Unio perakensis Preston, 1912 (non De Morgan, 1885), p. 287, pl. 8, fig. 5–6.
 Type locality: 'Perak' [Perak State, Malaysia, 4.71822, 100.94497].
 Type(s): Reg number 616/1. Remarks: Junior primary homonym of Unio perakensis De Morgan, 1885. Renamed Rectidens prestoni Simpson, 1914.
- Rectidens prestoni Simpson, 1914, p. 1159. Remarks: Replacement name for Unio perakensis Preston, 1912.

Taxonomic opinions since Haas (1969a)

- Rectidens lingulatus lingulatus Haas (1969a, p. 93).
- Rectidens lingulatus prolongatus Haas (1969a, p. 94).
- Rectidens sumatrensis sumatrensis Haas (1969a, p. 94).
- Rectidens sumatrensis perakensis Haas (1969a, p. 95).
- Rectidens sumatrensis gracilis Haas (1969a, p. 95).
- Rectidens sumatrensis pressirostris Haas (1969a, p. 95).
- Rectidens prolongatus Haas (1969b, N434, fig. D32:7).
- Rectidens gracilis Marwoto (1987, p. 306).
- Rectidens sumatrensis Graf and Cummings (2007, p. 311), Affandi et al. (2014, p. 113, fig. 2D), Zieritz et al. (2016, p. 1071), Lopes-Lima et al. (2017, p. 177), Bolotov et al. (2017b, table S1; 2017a, p. 14, table S1), Zieritz et al. (2018a, online table 1; 2018b, p. 131), Razak et al. (2019, p. 459), Pfeiffer et al. (2018a, p. 410), Konopleva et al. (2019a, table S1; 2019b, appendix 1), Huang et al. (2019, table S4), Pfeiffer et al. (2019, p. 116), Zieritz et al. (2020, p. 2237), Bolotov et al. (2020, table S1), Lopes-Lima et al. (2020, table 1).
- Rectidens lingulatus Graf and Cummings (2007, p. 311), Zieritz et al. (2018a, online table 1).

Material examined

70 lots (Table S1).



Fig. 26. Representative specimens of *Rectidens sumatrensis*, *Prohyriopsis stolata*, *Elongaria orientalis*, *E. trompi*, *Ctenodesma borneensis* and ?C. scheibeneri.

Diagnosis

Same as for genus.

Distribution

Malay Peninsula and the islands of Sumatra, Java and Borneo (Fig. 21).

Ecoregions

Malay Peninsula Eastern Slope, Northern Central Sumatra–Western Malaysia, Southern Central Sumatra, Southern Sumatra–Western Java, South-eastern Borneo, Kapuas, North-western Borneo.

Remarks

Rectidens sumatrensis is the only Rectidentini known to occur on both mainland South-east Asia and the Malay Archipelago. The low genetic divergences between mainland South-east Asian populations and those on Borneo (Fig. 27) suggest that the species has undergone a large and relatively recent geographic expansion (Zieritz *et al.* 2020). Among the Contradentini, the only species known to occur on mainland South-east Asia and the Malay Archipelago are *L. contradens* and *P. superbus*.

Genus Ctenodesma Simpson, 1900

- Ctenodesma Simpson, 1900: 852. Type species: Unio borneensis Issel, 1874 by original designation.
- Christadens Simpson, 1914: 1154. Unnecessary replacement for Ctenodesma Simpson, 1900.

Diagnosis

This taxon is unlikely to be monophyletic and we are unable to provide a useful generic diagnosis.

Distribution

Borneo.



Fig. 27. COI gene tree of Hyriopsis and Rectidens. Nodal support (UFBoot) is listed above branches.

Species

We recognise two valid species in the genus *Ctenodesma* (Fig. 26).

- Ctenodesma borneensis (Issel, 1874).
- ?Ctenodesma scheibeneri Haas, 1927.

Remarks

The monophyly of this genus is untested and unlikely. Morphologically, *Ctenodesma borneensis* resembles other Rectidentini and recent molecular phylogenetic reconstructions recover that taxon as sister to the rest of the Rectidentini, albeit with limited support (Zieritz *et al.* 2020). *?Ctenodesma scheibeneri* is morphologically quite different from *C. borneensis* and most other Rectidentini in that it has strongly fractured pseudocardinal teeth (*v.* lamelliform), distinct green rays (*v.* blurry), and more circular shell outline (*v.* elongate) (Fig. 26).

Ctenodesma borneensis (Issel, 1874)

(Table 1; Fig. 1, 10, 26–28; Tables S1, S2)

- Unio plicatulus Lea, 1859 (non Küster, 1856), p. 152 figured in Lea 1860a, p. 247, pl. 37, fig. 126. *Type locality*: 'Borneo'. *Type(s)*: holotype by monotypy, NHMUK 1965156 (Johnson 1971, p. 91). *Remarks*: Junior primary homonym of *Unio plicatulus* Küster, 1856. Renamed *Unio borneensis* Issel, 1874.
- Unio borneensis Issel, 1874, p. 113. Remarks: Replacement name for Unio plicatulus Lea, 1859.
- Unio pensitatus Fischer & Crosse, 1894, p. 599. Remarks: Unnecessary replacement for Unio plicatulus Lea, 1859.

Taxonomic opinions since Haas (1969a)

- Ctenodesma borneensis Haas (1969a, p. 78), Graf and Cummings (2007, p. 310), Zieritz *et al.* (2018*b*, p. 131; 2018*a*, online table 1), Zieritz *et al.* (2020, p. 2237).
- Ctenodesma borneense Haas (1969b, N420, fig. D20:1), Starobogatov (1970, p. 60).

Material examined

11 lots (Table S1).

Diagnosis

Ctenodesma borneensis resembles *Rectidens sumatrensis* but has yellow periostracum and has more sculpturing on the shell disc and posterior slope.

Distribution

Western and northern Borneo (Fig. 28).

Ecoregions

Kapuas, North-eastern Borneo, North-western Borneo.

Remarks

Von Martens (1867) listed this species from north-western Borneo, coastal areas near Mempawah, and Danau Seriang. However, the specimens from Mempawah and Danau Seriang were not located in our museum sampling and therefore are not included in the map (Fig. 28). Issel (1874) listed north-east Borneo in the distribution of this species but this appears to be an incorrect translation of von Martens (1867).

Despite significant recent sampling efforts in northern Borneo this species has been found at only one site (Zieritz *et al.* 2018*b*, 2020).

?Ctenodesma scheibeneri Haas, 1927

(Table 1; Fig. 1, 10, 26, 28; Table S1)

Ctenodesma scheibeneri Haas, 1927, p. 20, pl. 1, fig. 1. Type locality: 'Borneo, Oberlauf des Soengei Batoe, Kp. Moeara Koeajan, Unterabt. Sampit, U. Distr. Boven-Sampit' [Mentaya River, Sampit, Central Kalimantan Province, Borneo, Indonesia, -2.53900, 112.96632]. Type(s): holotype by monotypy, SMF 3283 (Zilch 1967, p. 87).

Taxonomic opinions since Haas (1969a)

Ctenodesma scheibeneri – Haas (1969a, p. 78), Graf and Cummings (2007, p. 310), Zieritz *et al.* (2018a, online table 1), Zieritz *et al.* (2020, p. 2237).

Material examined

1 lot (Table S1).

Diagnosis

?Ctenodesma scheibeneri is diagnosed by its strongly fractured pseudocardinal teeth, fine and distinct green rays, sculptured shell disc, and more circular shell outline.

Distribution

Known only from the type locality in the Sampit drainage, southern Borneo (Fig. 28).

Ecoregion

South-eastern Borneo.

Remarks

The species has not yet been included in a molecular phylogeny.

Genus *Elongaria* Haas, 1911

Elongaria Haas, 1911: pl. 17. *Type species*: *Unio orientalis* Lea, 1840 by original designation.

Nannonaia Haas, 1913: 169. Type species: Unio trompi Drouët & Chaper, 1892 by monotypy.

Diagnosis

This taxon is unlikely to be monophyletic, and we are unable to provide a useful generic diagnosis.

Distribution

Known only from Borneo and Java.

Species

We recognise two valid species in the genus *Elongaria* (Fig. 26).

- Elongaria orientalis Haas, 1911.
- ?Elongaria trompi (Drouët & Chaper, 1892).



Fig. 28. Dot distribution map of *Ctenodesma borneensis*, ?*Ctenodesma scheibeneri*, *Elongaria orientalis* and ?*Elongaria trompi*.

Remarks

The monophyly of this genus is untested and unlikely. *Elongaria orientalis* is morphologically very similar to *Rectidens* and appears to be closely related to that genus (or is potentially a junior synonym of that genus) (Fig. 26). *?Elongaria trompi* has shell sculpturing that is unlike all other Rectidentini, and its position among the Rectidentini has recently been questioned (Pfeiffer *et al.* 2018*a*).

Elongaria orientalis (Lea, 1840)

(Table 1; Fig. 1, 10, 26, 28; Table S1)

- Unio orientalis Lea, 1840, p. 285 figured in Lea 1842, p. 221, pl. 18, fig. 38. Type locality: 'Java?' [Java, Indonesia, not fixed]. Type(s): lectotype, USNM 86058 (Johnson 1974, p. 104, as the holotype).
- Unio productus Mousson, 1849 (non Conrad, 1836), p. 93, pl. 17, fig. 3–5. Type locality: 'rührt aus der Gegand von Pardana' [Pardana, Java, Indonesia, not fixed]. Type(s): unknown. Remarks: Junior primary

homonym of Unio productus Conrad, 1836. Renamed Unio production Lea, 1852.

- Unio productior Lea, 1852, p. 29. Remarks: Replacement name for Unio productus Mousson, 1849.
- Unio bithynicus Kobelt, 1893, p. 96, pl. 179, fig. 1128. Type locality: 'im vorderen Kleinasien' [Asia Minor, dubious]. Type(s): unknown. Remarks: According to Haas (1940, p. 141), 'Not from Asia Minor, as believed by Kobelt, being nothing but Elongaria orientalis Lea from Java.'

Taxonomic opinions since Haas (1969a)

Elongaria (s.s.) orientalis – Haas (1969a, p. 79; 1969b, N423, fig. D21:4).
Elongaria orientalis – Graf and Cummings (2007, p. 310), Affandi et al. (2014, p. 113, fig. 2C), Zieritz et al. (2018a, online table 1).

Material examined

17 lots (Table S1).

Diagnosis

Distinguishing *Elongaria orientalis* from *Rectidens* sumatrensis using shell characters is very difficult but *E. orientalis* tends to have a brighter periostracum (greenish-yellow to brown) than *R. sumatrensis* (brown to black).

Distribution

Restricted to Java (Fig. 28).

Ecoregions

Southern Sumatra-Western Java, Central & Eastern Java.

Remarks

Elongaria orientalis is the only Contradentini or Rectidentini thought to be endemic to the island of Java. However, the validity of this taxa is uncertain, and it may be a junior synonym of *Rectidens sumatrensis*. The species has not yet been included in a molecular phylogeny.

?Elongaria trompi (Drouët & Chaper, 1892)

(Table 1; Fig. 1, 26, 28; Table S1)

Unio trompi Drouët & Chaper, 1892, p. 153, pl. 6, fig. 8–10. Type locality: 'Le Kapoeas (Semitau), a Borneo' [Kapuas River, Semitau, West Kalimantan Province, Borneo, Indonesia, 0.55548, 111.96045]. Type(s): syntypes, MCZ 174098 (n = 1) (Johnson 1956, p. 139, as a cotype); SMF 3178 (n = 2) (Zilch 1967, p. 88); MNHN-IM-2000–1805 (n = 1).

Taxonomic opinions since Haas (1969a)

- *Elongaria (Nannonaia) trompi* Haas (1969b, N423, fig. D21:5; 1969a, p. 80).
- *Elongaria trompi*-Graf and Cummings (2007, p. 310), Pfeiffer *et al.* (2018*a*, p. 414), Zieritz *et al.* (2018*a*, online table 1), Zieritz *et al.* (2020, p. 2238).

Material examined

11 lots (Table S1).

Diagnosis

Elongaria trompi is distinguished from other Rectidentini by its slightly concave ventral margin and sculpturing on the shell disc.

Distribution

Kapuas drainage in western Borneo (Fig. 28).

Ecoregion

Kapuas.

Remarks

This taxon shares several traits with representatives of the tribe Indochinellini (Subfamily Parreysiinae), including its small size, slightly concave ventral margin, and fine zig-zag sculpturing on the shell disc, and may belong to that tribe (Pfeiffer *et al.* 2018*a*). If so, the generic name *Nannonaia* Haas, 1913 may be valid, and the Nannonaiini Modell, 1942 would have priority over the Indochinellini Bolotov, Pfeiffer, Vikhrev & Konopleva in Bolotov *et al.* (2018). The Indochinellini is distributed across much of Indochina and the Malay Peninsula, but is not yet known to occur on the Malay Archipelago. Testing the phylogenetic position of *?Elongaria trompi* has important biogeographic and nomenclatural implications. The species has not yet been included in a molecular phylogeny.

Genus Ensidens Frierson, 1911

Ensidens Frierson, 1911: 98. *Type species: Unio ingallsianus* Lea, 1852 by subsequent designation in Haas (1913, p. 139).

Diagnosis

Ensidens can be distinguished from other representatives of the Rectidentini by its very short and steep posterior slope. The posterior end tends to terminate more dorsally in *Ensidens*, whereas in *Rectidens* the posterior tends to terminate more ventrally (Fig. 10).

Distribution

Widespread in Indochina. Uncommon in the Malay Peninsula, and absent from Malay Archipelago.

Species

We recognise six valid species in the genus *Ensidens* (Fig. 29).

- Ensidens ingallsianus (Lea, 1852).
- Ensidens dugasti (Morlet, 1892), stat. rev.
- Ensidens jaculus (Rochebrune, 1882), stat. rev.
- Ensidens sagittarius (Lea, 1895).
- Ensidens spiculus, **sp. nov.**
- Ensidens telus, **sp. nov.**

Remarks

Ensidens is a morphologically conserved clade (Fig. 29) but is phylogenetically quite diverse (Fig. 30). Muanta *et al.* (2019) recently demonstrated that the species-level diversity of *Ensidens* is underestimated and a synthetic taxonomic revision of the clade is needed.

The genus can be divided into two clades, one of which is restricted to the Mekong drainage (and largely to just the Khorat Plateau) (Fig. 32), the other clade also occurs in the Mekong but is further distributed in the drainages to the west, and south down the Malay Peninsula (Fig. 31). These six species are largely allopatric but in a relatively short stretch of the Mekong River (~150 miles), near the confluence of the Songkhram River, there are four phylogenetically distinct but morphologically similar species of *Ensidens*. Distinguishing the *Ensidens* spp. from this area using shell characters is difficult to impossible, as indicated when comparing the diagnoses (or lack thereof) for each species.

Ensidens is unusual in comparison to most other Contradentini+Rectidentini in that we have observed it to be tetragenous or ectobranchous. Tetrageny is the more common of the brooding conditions in *Ensidens*, and it may be that 'ectobranchous' individuals were observed at an early or late developmental stage.

Many *Ensidens* species are named for their resemblance to various ranged weapons like arrows, spears, javelins, darts (latin – jaculum, spiculum, tellum, sagitta).

Ensidens ingallsianus (Lea, 1852)

(Tables 1, 3; Fig. 1, 9, 10, 29–31; Tables S1, S2; Fig. S1–S5)

- Unio ingallsianus Lea 1852, p. 282, pl. 24, fig. 41. Type locality: 'Siam' [Thailand, not fixed]. Type(s): holotype, USNM 85933 (Johnson 1974, p. 74).
- Unio pazii Lea, 1862, p. 176 figured in Lea 1866, p. 61, pl. 21, fig. 60. Type locality: 'China'. Type(s): holotype, USNM 84708 (Johnson 1974, p. 108). Remarks: Label with holotype reads 'Siam' [Thailand, not fixed].

Taxonomic opinions since Haas (1969a)

Ensidens (s.s.) ingallsianus [in part] – Haas (1969a, p. 72).

Ensidens (s.s.) ingallsianus - Haas (1969b, N423, fig. D21:1).

- Ensidens ingallsianus [in part] Woodward (1969, p. 49, pl. 1, fig. 1-2).
- Ensidens ingallsianus Graf and Cummings (2007, p. 310), Bogan and Do (2014, p. 113), Kongim et al. (2015, p. 98), Zieritz et al. (2016, p. 1071), Lopes-Lima et al. (2017, p. 177), Zieritz et al. (2018a, online table 1), Konopleva et al. (2019b, appendix 1), Pfeiffer et al. (2019, p. 116), Jeratthitikul et al. (2019, p. 137).
- *Ensidens cf. ingallsianus* Bolotov *et al.* (2017*a*, table S1; 2017*b*, table S1), Bolotov *et al.* (2018, table S1), Konopleva *et al.* (2019*a*, table S1), Huang *et al.* (2019, table S4), Zieritz *et al.* (2020, p. 2242), Bolotov *et al.* (2020, table S1).
- Ensidens ingallsianus ingallsianus [in part] Brandt (1974, p. 288, pl. 24, fig. 47).

Ensidens ingallsianus ingallsianus - Deein et al. (2004, p. 55).

Ensidens pazii – Konopleva *et al.* (2019*b*, appendix 1), Bolotov *et al.* (2020, table S1).

Ensidens ingallsianus A1 - Muanta et al. (2019, table S1).

Material examined

90 lots (Table S1).

Diagnosis

Ensidens ingallsianus has a posterior end that terminates more dorsally than that of other congeners. *Ensidens ingallsianus* also tends to be slightly more elongate and compressed in

comparison to its sister species, *E. telus*. However, all *Ensidens* species are morphologically very similar and are distinguished most easily by their cohesive geographic and genetic patterns.

Distribution

Widespread in the Mae Klong, Chao Phraya, and Bang Pakong drainages of western and central Thailand, as well as the coastal drainages of the Malay Peninsula. Disjunct populations also occur in the headwaters of the Mun watershed (Mekong drainage) (Fig. 31)

Ecoregions

Mae Klong, Chao Phraya, Eastern Gulf of Thailand Drainages, Khorat Plateau, North Central Sumatra–Western Malaysia, Malay Peninsula Eastern Slope.

Remarks

The type localities of Unio ingallsianus Lea, 1852 and Unio sagittarius Lea, 1856 are both 'Siam'. This ambiguity complicates determining what name belongs to what clade. This is especially unclear because the collector of these type specimens. William Haines, is known to have sampled from both the Chao Phraya and Mekong drainages and listed almost all specimens as simply being from 'Siam' (See L. contradens account for further discussion regarding this problem). It is our opinion that the holotype of Unio ingallsianus shares more similarities to samples collected from the Chao Phrava. including their more ovate shell shape and a posterior end that terminates dorsally. Whereas the lectotype of Unio sagittarius shares more similarities to samples collected from the Mun River watershed (Mekong drainage) including their more elongate shell shape and a posterior end that terminates centrally or ventrally.

This species is absent from much of the Mekong drainage and is restricted to two localities along the western edge of the Khorat Plateau ecoregion. This range disjunction and the shallow genetic divergences suggests that the Mun watershed may have recently captured portions of the Chao Phraya or the Bang Pakong drainages, or portions of both (Fig. 30, 31).

Ensidens dugasti (Morlet, 1892), stat. rev.

(Tables 1, 3; Fig. 1, 9, 29, 30, 32; Tables S1, S2; Fig. S1–S5)

Unio dugasti Morlet, 1892, p. 86 – figured in Morlet 1893, p. 156, pl. 6, fig. 4. Type locality: 'Riviere Outhene, petit affluent du Mekong dans le Laos' [Houtene, confluence of Nam Hinbourne and Mekong rivers, Khammouane Province, Laos, 17.58508, 104.60976]. Type(s): syntypes, NHMUK 1893.12.8.137–138 (n = 2) (Johnson 1971, p. 83, as paratypes).

Taxonomic opinions since Haas (1969a)

Ensidens (s.s.) sagittarius [in part] – Haas (1969*a*, p. 73). *Ensidens ingallsianus dugasti* – Brandt (1974, p. 288, pl. 24, fig. 48). *Ensidens sagittarius* B2 – Muanta *et al.* (2019, table S1). *Ensidens sagittarius* – Konopleva *et al.* (2019*b*, appendix 1).

Material examined

20 lots (Table S1).



Fig. 29. Representative specimens of *Ensidens*. Scale bar equals 1 inch (2.54 mm).

Diagnosis

Ensidens dugasti is very similar to *E. spiculus* and we did not observe any traits that were capable of distinguishing the two species. *Ensidens dugasti* is distinguished from *E. spiculus* most easily by their cohesive geographic and genetic patterns.

Distribution

Mekong drainage in Thailand and Laos. Populations concentrated in the Songkhram watershed but also occurs in other nearby watersheds of the Mekong (Fig. 32).

Ecoregion

Khorat Plateau.

Remarks

Ensidens dugasti appears to be the most geographically restricted and genetically homogenous *Ensidens* species.

Ensidens jaculus (Rochebrune, 1882), stat. rev.

(Tables 1, 3; Fig. 1, 9, 29, 30, 32; Tables S1, S2; Fig. S1–S5)

Unio jaculus Rochebrune, 1882, p. 44. Type locality: 'Rapides de Sombor' [Mekong River, Sombour, Sambour District, Kratié Province, Cambodia, 12.77440, 105.96311]. Type(s): syntype, MNHN-IM-2000-1724.

Taxonomic opinions since Haas (1969a)

Ensidens (s.s.) sagittarius [in part] – Haas (1969*a*, p. 72). *Ensidens sagittarius* – Do *et al.* (2018, p. 5). table S1).

Ensidens ingallsianus ingallsianus [in part] – Brandt (1974, p. 288).
Ensidens sp. – Lopes-Lima et al. (2017, p. 177), Zieritz et al. (2020, p. 2242).
Ensidens sp. 1 – Bolotov et al. (2017a, p. 13, table S1; 2017b, table S1), Bolotov et al. (2018, table S1), Konopleva et al. (2019a, table S1;

2019b, appendix 1), Huang et al. (2019, table S4), Bolotov et al. (2020,

Ensidens sp. 2 – Konopleva *et al.* (2019*b*, appendix 1), Bolotov *et al.* (2020, table S1).

Ensidens ingallsianus [in part] – Do *et al.* (2018, p. 5, Table 2). *Ensidens sagittarius* B3 – Muanta *et al.* (2019, table S1).



Fig. 30. COI gene tree of Ensidens. Nodal support (UFBoot) is listed above branches.



Fig. 31. Dot distribution map of *Ensidens ingallsianus* and *E. telus*.

Material examined 21 lots (Table S1).

Diagnosis

Ensidens jaculus may be slightly less elongate than its sister species, *E. spiculus*. However, all *Ensidens* species are morphologically very similar and are distinguished

most easily by their cohesive distributional and genetic patterns.

Distribution

Mekong drainage in Thailand, Laos, and Cambodia (Fig. 32).

Ecoregion

Khorat Plateau, Kratie-Stung Treng.

Remarks

Majority of records are from the Mekong River proper or nearby tributaries.

Ensidens sagittarius (Lea, 1856)

(Tables 1, 3; Fig. 1, 9, 29, 30, 32; Tables S1, S2; Fig. S1–S5)

Unio sagittarius Lea 1856, p. 93 – figured in Lea 1857, p. 298, pl. 26, fig. 12. *Type locality*: 'Siam' [Thailand, not fixed]. *Type(s)*: lectotype, USNM 85934 (Johnson 1974, p. 127, as the holotype).

Taxonomic opinions since Haas (1969a)

Ensidens (s.s.) sagittarius [in part] - Haas (1969a, p. 72).

Ensidens ingallsianus ingallsianus [in part] – Brandt (1974, p. 288).

Ensidens sagittarius – Graf and Cummings (2007, p. 310), Zieritz *et al.* (2018*a*, online table 1), Konopleva *et al.* (2019*b*, appendix 1), Huang *et al.* (2019, table S4), Muanta *et al.* (2019, p. 224), Zieritz *et al.* (2020, p. 2242), Bolotov *et al.* (2020, table S1), Lopes-Lima *et al.* (2020, table 1).

Ensidens aff. *sagittarius* sp. 3 – Bolotov *et al.* (2017*a*, p. 13, table S1; 2017*b*, table S1), Bolotov *et al.* (2018, table S1), Konopleva *et al.* (2019*a*, table S1; 2019*b*, appendix 1), Huang *et al.* (2019, table S4), Zieritz *et al.* (2020, p. 2242).

Ensidens sagittarius B1– Muanta *et al.* (2019, table S1). *Ensidens* sp. 'Mun' – Bolotov *et al.* (2020, table S1).

Material examined

36 lots (Table S1).

Diagnosis

Ensidens sagittarius is typically more elongate than *E. ingallsianus* and *E. telus* but we unable to use morphological characters to distinguish this species from the other Mekong endemic *Ensidens*. All *Ensidens* species are morphologically very similar and are distinguished most easily on the basis cohesive of their cohesive geographic and genetic patterns

Distribution

Mekong drainage in Thailand and Laos (Fig. 32).

Ecoregion

Khorat Plateau.

Remarks

Most records are from the Mun watershed, but the species does occur in the Mekong proper, including one geographically divergent population >150 river miles upstream of the nearest population.

Ensidens spiculus, sp. nov.

(Tables 1, 3; Fig. 1, 9, 29, 30, 32; Tables S1, S2; Fig. S1–S5)

Type locality

Mekong River, along Rt. 211, Sangkhom District, Nong Khai Province, Thailand, 18.11106, 102.22679.

Types

Holotype, UF 564752. Paratype, UF 507755 (n = 1), same locality as the holotype.

Taxonomic opinions since Haas (1969a)

Ensidens aff. *sagittarius* sp. 2 – Bolotov *et al.* (2017*a*, p. 13, table S1; 2017*b*, table S1), Bolotov *et al.* (2018, table S1), Konopleva *et al.* (2019*a*, table S1; 2019*b*, appendix 1), Huang *et al.* (2019, table S4), Zieritz *et al.* (2020, p. 2242).

Ensidens sagittarius B4 – Muanta *et al.* (2019, table S1). *Ensidens* sp. 'Thai' – Bolotov *et al.* (2020, table S1).

Material examined

12 lots (Table S1).

Diagnosis

Ensidens spiculus is very similar to *E. dugasti*, and we did not observe any traits that were capable of distinguishing the two species. *Ensidens spiculus* is distinguished from *E. dugasti* most easily on the basis of cohesive geographic and genetic patterns.

Description

Shell elongate, moderately thick, somewhat inflated. Anterior end narrow, broadly rounded. Posterior end elongate, bluntly pointed. Dorsal and ventral margins slightly curved. Posterior slope very steep, especially near the umbo. Periostracum light yellow to brown. Umbo not elevated above the hinge line. Nacre iridescent, faintly blueish-purple, opaque, strong striations. Pseudocardinal and lateral teeth in slight arch, blade-like, coarse texture. Left valve with two lateral teeth, curved, slightly sinuous in large specimens. Left valve with one pseudocardinal tooth, triangular accessory tooth at the posterior end. Right valve with one lateral tooth, slightly curved. Right valve with two pseudocardinal teeth, ventral tooth much larger than dorsal. Supra-anal aperture, excurrent aperture and pallial fusion between of similar length. Excurrent aperture smooth, slightly smaller than incurrent. Incurrent aperture with multiple rows of short simple, conical-shaped papillae. Tetragenous brooding (occasionally ectobranchous). Gills laterally swollen when gravid. Septa with small perforations. Unhooked glochidia.

Distribution

Mekong drainage in Thailand and Laos. (Fig. 32).

Ecoregions

Lower Lancang, Khorat Plateau.

Remarks

This is the only species of *Ensidens* known to occur in the Lower Lancang ecoregion.

Ensidens telus, sp. nov.

(Tables 1, 3; Fig. 1, 9, 29–31; Tables S1, S2; Fig. S1–S5)

Type locality

Tonle Sap River, near Phumi Trâpeang Préal, Kampong Chhnang Province, Cambodia, 12.05848, 104.77307.

Types

Holotype, UF 564753. Paratypes, UF 507435 (n = 37), same locality as the holotype.



Fig. 32. Dot distribution map of E. sagittarius, E. jaculus, E. dugasti and E. spiculus.

Taxonomic opinions since Haas (1969a)

- *Ensidens sagittarius* Pfeiffer and Graf (2015, p. 310), Lopes-Lima *et al.* (2017, p. 177), Konopleva *et al.* (2017, p. 207).
- *Ensidens* aff. *sagittarius* sp. 1 Bolotov *et al.* (2017*a*, p. 13, table S1; 2017*b*, table S1), Bolotov *et al.* (2018, table S1), Konopleva *et al.* (2019*a*, table S1), Huang *et al.* (2019, table S4), Zieritz *et al.* (2020, p. 2242), Lopes-Lima *et al.* (2020, table 1).

Ensidens ingallsianus A2 – Muanta et al. (2019, table S1).

Ensidens ingallsianus – Konopleva *et al.* (2019*b*, appendix 1), Bolotov *et al.* (2020, table S1).

Material examined 46 lots (Table S1).

Diagnosis

Ensidens telus is the least elongate species of *Ensidens*. However, all *Ensidens* species are morphologically very similar and are distinguished most easily by cohesive biogeographic and genetic patterns.

Description

Shell elongate oval, moderately thick-shelled, somewhat inflated. Anterior end narrow, broadly rounded. Posterior end elongate, bluntly pointed. Dorsal and ventral margins rounded. Posterior slope steep, especially near the umbo. Umbo slightly elevated above the hinge line. Nacre iridescent, faintly blueishpurple, opaque, strong striation, tan to orangish tint near umbo. Left valve with two lateral teeth, curved, coarse texture. Left valve with one pseudocardinal tooth, occasionally with accessory dentition at the posterior end. Right valve with one lateral tooth, curved. Right valve with two pseudocardinal teeth, ventral tooth longer than dorsal. Supra-anal aperture short. Pallial fusion between supra-anal and excurrent 2× longer than supraanal aperture. Excurrent aperture smooth, smaller than incurrent. Incurrent aperture with multiple rows of short simple, conicalshaped papillae. Tetragenous brooding. Marsupium laterally swollen and slightly blush when glochidia fully developed. Perforated septa, perforation width approximately equal to connection width. Semielliptical unhooked glochidia

Distribution

Widespread in Mekong drainage in western Cambodia and southern Vietnam. Also known from the Bang Pakong and Chantaburi drainages of south-eastern Thailand and Soai Rap drainage of southern Vietnam (Fig. 31).

Ecoregions

Chao Phraya, Eastern Gulf of Thailand Drainages, Mekong Delta.

Remarks

This species is known primarily from the Mekong drainage but it is also known from a few localities along the western edge of the Chao Phraya ecoregion. This range disjunction and the shallow genetic divergences suggest that the Bang Pakong may have recently captured portions of the Mekong (Fig. 30, 31).

Genus Hyriopsis Conrad, 1853

Hyriopsis Conrad, 1853: 267. *Type species: Unio delphinus* Gruner, 1841 non Spengler, 1793 by monotypy.

Diagnosis

Hyriopsis can be distinguished from all other Contradentini +Rectidentini by its large posterior wing (Fig. 10).

Distribution

Widespread in mainland South-east Asia. From the Mae Klong drainage in the west to the Mekong drainage in the east, and south across the Malay Peninsula. A few records from Sumatra (2) and Borneo (1).

Species

We recognise nine valid species and one undescribed species in the genus *Hyriopsis* (Fig. 33).

- Hyriopsis bialata Simpson, 1900.
- Hyriopsis delaportei (Crosse & Fischer, 1876).
- Hyriopsis desowitzi Brandt, 1974.

- Hyriopsis myersiana (Lea, 1856).
- Hyriopsis kratiensis, sp. nov.
- Hyriopsis phuphaniensis, sp. nov.
- Hyriopsis khoratensis, sp. nov.
- Hyriopsis sakhonensis, **sp. nov.**
- *Hyriopsis* undescribed.
- Hyriopsis velthuizeni (Schepman, 1896).

Remarks

Several recent multilocus phylogenies have recovered *Hyriopsis* as non-monophyletic (Zieritz *et al.* 2016, 2020; Lopes-Lima *et al.* 2017; Pfeiffer *et al.* 2018*a*). However, our phylogenomic reconstruction strongly supports the monophyly of the genus (Fig. 9). Our phylogenomic reconstruction also finds strong support for a multispecies Mekong radiation including *H. kratiensis*, *H. khoratensis* and *H. sakhonensis* (*H. phuphaniensis* also belongs to this clade but was not included in our phylogenomic analysis). This Mekong radiation is not recovered in our *COI* gene tree (Fig. 27).

Limnoscapha Lindholm, 1932 has recently been treated as a subgenus (Kittivorachate and Yangyuen 2004; Deein *et al.* 2004) or junior synonym of *Hyriopsis* Simpson, 1900 (Graf and Cummings 2006*a*; Vinarski 2019) but we follow Do *et al.* (2018) who suggested that *Limnoscapha* Lindholm, 1932 represents a distantly related fossil taxon distinct from *Hyriopsis*.

Common names for species of *Hyriopsis* are loosely translated in English as 'two-winged clam', 'hatchet clam' and 'flying boat clam' (Nabhitabhata 2009).

Hyriopsis bialata Simpson, 1900

(Tables 1, 3; Fig. 1, 9, 10, 27, 33, 34; Tables S1, S2; Fig. S1–S5)

- Unio delphinus Lea, 1840 (non Spengler, 1973), p. 285 figured in Lea 1842, p. 218, pl. 17, fig. 35. *Type locality:* 'New Holland' [Australia, dubious]. *Type(s):* holotype, USNM 83910 (Johnson 1974, p. 45). *Remarks:* Junior primary homonym of Unio delphinus Spengler, 1793.
- Unio delphinus Gruner, 1841 (non Spengler, 1973), p. 276, p. 11, fig. 1–1c. Type locality: 'Songi flumine Malaccae' [Songi River, Malacca, Malaysia, 2.17968, 102.22665]. Type(s): syntypes, MCZ 186371 (n = 2) (Johnson 1956, p. 112, as a cotypes); ANSP 56588 (n = 2) (Johnson 1980, p. 277, as a paratype). Remarks: Junior primary homonym of Unio delphinus Spengler, 1793. Renamed Hyriopsis bialatus Simpson, 1900.
- Unio megapterus Morelet, 1864 (non Rafinesque, 1820), p. 159. Type locality: 'Conchinchina' [Vietnam, not fixed]. Type(s): unknown. Remarks: Junior secondary homonym of Metaptera megaptera Rafinesque, 1820.
- *Hyriopsis bialatus* Simpson, 1900, p. 579. *Remarks*: Replacement name for *Unio delphinus* Gruner, 1841.
- Unio delphinopterus Dautzenberg & Fisher, 1905, p. 456. Remarks: Dautzenberg and Fischer (1905) regarded Hyriopsis bialatus Simpson to be preoccupied by Deshayes in Lamarck (1835) placement of Symphynota bialata Lea in Unio. ICZN Art. 59.3 is clear that since these species are no longer secondary homonyms and the replacement (before 1961) is not in common usage, this is an unnecessary replacement for Hyriopsis bialatus Simpson, 1900.
- Hyriopsis gracilis Haas, 1910, p. 101. Type locality: Bienho-Sei, Mekong [Bien Ho Lake, Vietnam, 14.052075, 108.000377]. Type(s): SMF 3577 (destroyed during war) (Solem 1967, p. 113).



Fig. 33. Representative specimens of Hyriopsis. Scale bar equals 1 inch (2.54 mm).



Fig. 34. Dot distribution map of *Hyriopsis bialata*, *H. myersiana* and *Prohyriopsis stolata*. Question marks highlight questionable records – see remarks in *H. myersiana* account.

Taxonomic opinions since Haas (1969a)

Hyriopsis bialata – Haas (1969a, pp. 147–148; 1969b, N423, fig. D23:2), Graf and Cummings (2007, p. 310), Zieritz et al. (2016, p. 1071, appendix S2), Bolotov et al. (2017a, p. 14, table S1; 2017b, table S1), Zieritz et al. (2018a, online table 1), Razak et al. (2019, p. 459), Pfeiffer et al. (2019, p. 116), Huang et al. (2019, table S4), Lopes-Lima et al. (2020, table 1), Zieritz et al. (2020, p. 2242). Hyriopsis (s.s.) bialatus - Brandt (1974, p. 272, pl. 21, fig. 36).

- *Hyriopsis bialatus* Graf (2007, p. 87), Sri-aroon *et al.* (2007, p. 298), Bogan and Do (2014, p. 113), Kongim *et al.* (2015, p. 98), Do *et al.* (2018, p. 8), Konopleva *et al.* (2019*a*, table S1; 2019*b*, appendix 1), Bolotov *et al.* (2020, table S1).
- *Hyriopsis gracilis* Do *et al.* (2018, p. 8, table 2), Konopleva *et al.* (2019*b*, appendix 1), Zieritz *et al.* (2020, p. 2243), Bolotov *et al.* (2020, table S1).

Material examined

83 lots (Table S1).

Diagnosis

Hyriopsis bialata is the most elongate and dorsoventrally compressed species of *Hyriopsis*.

Distribution

Disjunct distribution in Mekong drainage in Cambodia and Vietnam and the southern Malay Peninsula (Fig. 34).

Ecoregions

North Central Sumatra–Western Malaysia, Malay Peninsula Eastern Slope, Mekong Delta.

Remarks

The few records of *H. bialata* from the Philippines (UF 270731, USNM 7664) and India (USNM 25679) are likely to have incorrect locality information and were omitted from our analyses.

Despite the large geographic distance between *H. bialata* populations in the Malay Peninsula and the Tonle Sap (Fig. 34), the sequenced individuals are very closely related (Fig. 27). The large geographic disjunction and limited genetic diversity observed in *H. bialata* is quite unusual but a similar pattern is known from at least one other freshwater mussel (Monodontina cambodjensis (Petit, 1865) - compare individuals associated with GenBank accessions KP795028 and KX051297). The Mekong drainage is not typically associated with the Paleo-Siam River but parts of western Cambodia, and perhaps parts of the modern-day Tonle Sap watershed, may have drained into the Gulf of Thailand and been connected to the Paleo-Siam River (Rainboth 1996; Attwood and Johnston 2001; Adamson et al. 2012). The species may have recently undergone a major geographic expansion associated with the Paleo-Siam River with subsequent extinction across much of its range (e.g. Eastern Gulf of Thailand, Chao Phraya, Mae Klong and most of the Malay Peninsula Eastern Slope ecoregions). An alternative explanation could be non-native introduction to the Malay Peninsula.

Hyriopsis delaportei (Crosse & Fischer, 1876)

(Tables 1, 3; Fig. 1, 9, 27, 33, 35; Tables S1, S2; Fig. S1–S5)

Unio (Arconaia) delaportei Crosse & Fischer, 1876, p. 327, pl. 10, fig. 1; pl. 11, fig. 5. Type locality: 'Compong-Soai dista, Cambodgiæ' [Kampong Siem (Mekong Drainge), Kampong Cham Province, Cambodia, 12.00176, 105.46848]. Type(s): syntype, MNHN-IM-2000–1671.

Taxonomic opinions since Haas (1969a)

- Hyriopsis delaportei [in part] Haas (1969a, p. 148).
- *Hyriopsis delaportei* Graf and Cummings (2007, p. 310), Bogan and Do (2014, p. 113, fig. 1), Do *et al.* (2018, p. 9, table 2), Zieritz *et al.* (2018*a*, online table 1), Muanta *et al.* (2019, p. 225).

Hyriopsis (s.s.) delaportei - Brandt (1974, p. 273, pl. 21, fig. 37).

Material examined

16 lots (Table S1).

Diagnosis

Hyriopsis delaportei is most similar to its sister taxon, *H. desowitzi*, but is less inflated and has strong concentric ridges on the umbo.

Distribution

Mekong drainage in western Cambodia (Fig. 35).

Ecoregion

Mekong Delta.

Remarks

This species exhibits substantial amounts of ontogenetic variation. Small individuals are very thin-shelled with delicate teeth and ridges on the umbo whereas adults are quite robust with strongly flattened and fractured pseudocardinals.

Hyriopsis desowitzi Brandt, 1974

(Table 1; Fig. 1, 27, 33, 35; Tables S1, S2)

Hyriopsis (Limnoscapha) desowitzi Brandt, 1974, p. 274, pl. 22, fig. 43. Type locality: 'Klong Rapipat at Ban Ta Luang, in Ayutthia Province, W of Saraburi' [Khlong Raphi Phat, Ban Tha Luang, Phra Nakhon Si Ayutthaya Province, Thailand, 14.55464, 100.76260]. Type(s): holotype, MCZ 280894 (Zilch 1983, p. 84).

Taxonomic opinions since Haas (1969a)

Hyriopsis (Limnoscapha) desowitzi – Brandt (1974, p. 274, pl. 22, fig. 43).
Hyriopsis desowitzi – Graf and Cummings (2007, p. 310), Zieritz et al. (2016, appendix S2), Lopes-Lima et al. (2017, p. 177), Bolotov et al. (2017a, p. 14, table S1; 2017b, table S1), Zieritz et al. (2018a, online table 1), Bolotov et al. (2018, table S1), Muanta et al. (2019, p. 225), Huang et al. (2019, table S4), Konopleva et al. (2019a, table S1; 2019b, appendix 1), Zieritz et al. (2020, p. 2242), Bolotov et al. (2020, table S1).

Material examined

27 lots (Table S1).

Diagnosis

Hyriopsis desowitzi is most similar to its sister taxon, *H. delaportei*, but has a much more circular shell outline and is more inflated.

Distribution

Chao Phraya and Bang Pakong drainages of south-central and south-eastern Thailand (Fig. 35).

Ecoregion

Chao Phraya.

Hyriopsis myersiana (Lea, 1856)

(Tables 1, 3; Fig. 1, 9, 27, 33, 34; Tables S1, S2; Fig. S1–S5)

- Unio myersianus Lea, 1856, p. 92 figured in Lea 1857, p. 290, pl. 22, fig. 2. Type locality: 'Siam' [Thailand, not fixed]. Type(s): lectotype, USNM 83950 (Johnson1974: 95, as the holotype).
- *Unio housei* Lea, 1856, p. 92 figured in Lea 1857, p. 291, pl. 23, fig. 3. *Type locality*: 'Siam' [Thailand, not fixed]. *Type(s)*: lectotype, USNM 83951 (Johnson1974: 71, as the holotype).

- Unio sutrangensis Morlet, 1889. Page 195, pl. 9, fig. 3. Type locality: 'Rivière de Sutrang (Siam)' [Sutrang River (Mekong Drainage), Sa Kaeo Province, Thailand, 13.68877, 102.49712]. Type(s): unknown.
 - *Unio stungtrangensis* Fischer & Dautzenberg, 1904, p. 440. *Remarks*: Unjustified emendation *Unio sutrangensis* Morlet, 1889.
 - Unio patrangensis Morlet, 1904, p. 382. Remarks: Unjustified emendation Unio sutrangensis Morlet, 1889.

Taxonomic opinions since Haas (1969a)

Hyriopsis myersiana – Haas (1969a, p. 149), Graf and Cummings (2007, p. 310), Zieritz et al. (2016, appendix S2), Bolotov et al. (2017a, p. 14, table S1; 2017b, p. table S1), Lopes-Lima et al. (2017, p. 177), Zieritz et al. (2018a, online table 1), Bolotov et al. (2018, table S1), Muanta et al. (2019, p. 225), Huang et al. (2019, table S4), Konopleva et al. (2019a, table S1; 2019b, appendix 1), Bolotov et al. (2020, table S1), Zieritz et al. (2020, p. 2243).

Hyriopsis delaportei [in part] - Haas (1969a, p. 148).

Hyriopsis (Limnoscapha) myersiana – Brandt (1974, p. 275, pl. 22, fig. 44), Deein *et al.* (2004, p. 55).

Hyriopsis delaportei – Muanta et al. (2019, table S1).

Material examined

122 lots (Table S1).

Diagnosis

Hyriopsis myersiana has a more ovate shell outline and a smaller posterior wing in comparison to other *Hyriopsis*.

Distribution

Widespread in Mae Klong, Chao Phraya, and Bang Pakong drainages in Thailand (Fig. 34).

Ecoregions

Mae Klong, Chao Phraya.

Remarks

Unio sutrangensis Morlet, 1889 is described from 'Riviere de Sutrang (Siam)', which is a tributary of the Tonle Sap and is one of two questionable records of *H. myersiana* from the Mekong drainage (Fig. 34). However, Morlet (1904) emended the name Unio sutrangensis to Unio patrangensis so that it reflected the correct collection locality, Patrang, which is part of the Bang Pakong drainage. Morlet's (1904) emendation of Unio sutrangensis is unjustified but it is useful in that it raises further doubts concerning the presence of this species in the Mekong.

The other questionable record corresponds to a published *COI* sequence (MG025691) identified as *H. delaportei* and allegedly collected from the Mun watershed (Muanta *et al.* 2019). That sequence was recovered within our *H. myersiana* clade (Fig. 27) and it either represents a highly unusual disjunction or the metadata associated with this sequence is erroneous.

Hyriopsis kratiensis, sp. nov.

(Tables 1, 3; Fig. 1, 9, 27, 33, 36; Tables S1, S2; Fig. S1–S5)

Type locality

Mekong River, 1.4 miles upstream of Sambour, Sambour, Kratié Province, Cambodia, 12.79458, 105.97255.

Types

Holotype, UF 564754. Paratypes, UF 507415 (n = 18), same locality as the holotype.

Material examined

26 lots (Table S1).

Diagnosis

Hyriopsis kratiensis is morphologically similar to *Hyriopsis phuphaniensis* but has a squarer posterior end and larger wing.

Description

Shell elongately ovate to rectangular with large wing, thickshelled, and compressed. Anterior end wide, broadly rounded. Posterior end angular. Dorsal margin consists of large, serrated wing, nearly as tall as shell disc. Ventral margin is straight to slightly curved. Biangulate posterior slope, wide, gradual. Umbo not elevated above hinge line. Nacre iridescent anteriorly, salmon towards umbo, opaque, strong striations. Left valve with two lateral teeth, slightly curved, textured margins. Left valve with one oblique tooth extending from umbo to anterior adductor muscle (in smaller individuals), otherwise strongly fractured surface. Right valve with one lateral tooth, slightly curved, textured. Right valve with two small oblique pseudocardinal teeth extending from umbo to anterior adductor muscle (in small individuals), otherwise strongly fractured surface. Supra-anal aperture greater than 5×1000 longer than pallial fusion between excurrent and supra-anal, smooth, tall. Excurrent aperture smooth, shorter than incurrent. Incurrent with 1-2 rows of short, conical-shaped papillae. Perforated septa, connections much smaller than perforations. Ectobranchous brooding. Laterally swollen and blush with fully developed glochidia. Semielliptical unhooked glochidia.

Distribution

Mekong drainage in southern Laos and eastern Cambodia (Fig. 36).

Ecoregions

Khorat Plateau, Kratie-Stung Treng.

Remarks

Known only from the Mekong drainage south of Mun River watershed.

Hyriopsis phuphaniensis, sp. nov.

(Table 1; Fig. 1, 27, 33, 36; Tables S1, S2)

Type locality

Mekong River, Mukdahan, at Muk River mouth, Mukdahan Province, Thailand, 16.54613, 104.73171.

Types

Holotype, UF 564755. Paratypes, UF 507832 (n = 2), same locality data as the holotype.



Fig. 35. Dot distribution map of Hyriopsis delaportei, H. desowitzi and Hyriopsis undescribed.

Material examined

9 lots (Table S1).

Diagnosis

Hyriopsis phuphaniensis is morphologically very similar to *Hyriopsis kratiensis* but tends to be less rectangular and more ovate.

Description

Shell elongately ovate, large wing, thick-shelled, and compressed. Anterior end wide, broadly rounded. Posterior

end bluntly pointed, angular. Large wing, nearly as tall as shell disc. Ventral margin is straight to slightly curved. Biangulate posterior slope, wide, gradual. Umbo not elevated above hinge line. Nacre iridescent anteriorly, salmon-coloured towards umbo, opaque, strong striations. Left valve with two lateral teeth, curved, textured margins. Left valve with one oblique tooth extending from umbo to anterior adductor muscle (in smaller individuals), otherwise strongly fractured surface. Right valve with one lateral tooth, slightly curved, textured. Right valve with two small oblique pseudocardinal teeth extending from umbo to anterior adductor muscle (in small individuals), otherwise strongly fractured surface.

Distribution

Mekong drainage in north-eastern Thailand and west-central Laos (Fig. 36).

Ecoregion

Khorat Plateau.

Remarks

This species is known only from the Mekong River proper near and north of the Phu Phani Range (Fig. 36).

Hyriopsis khoratensis, sp. nov.

(Tables 1, 3; Fig. 1, 9, 27, 33, 36; Tables S1, S2; Fig. S1–S5)

Type locality

Pao River, Kamalasai, at Rt 214 bridge, Kamalasai District, Kalasin Province, Thailand, 16.34022, 103.57584.

Types

Holotype, UF 564756. Paratypes, UF 507618 (n = 9), same locality data as the holotype.

Taxonomic opinions since Haas (1969a)

Hyriopsis bialata - Lopes-Lima et al. (2017, p. 177).

Hyriopsis sp. 2 – Zieritz *et al.* (2016, appendix S2), Bolotov *et al.* (2017*a*, p. 14, table S1; 2017*b*, table S1), Bolotov *et al.* (2018, table S1), Huang *et al.* (2019, table S4).

Hyriopsis gracilis – Konopleva *et al.* (2019*a*, table S1; 2019*b*, appendix 1), Zieritz *et al.* (2020, p. 2243), Bolotov *et al.* (2020, table S1).

Hyriopsis bialatus [in part] – Muanta et al. (2019, table S1).

Material examined

59 lots (Table S1).

Diagnosis

Hyriopsis khoratensis is conchologically similar to *Hyriopsis bialata* but is less elongate and more ovate.

Description

Shell ovate with large posterior wing, small anterior wing, thick shelled, somewhat inflated. Anterior end slightly sinuous to slightly rounded. Posterior end bluntly pointed. Dorsal margin consists of large smooth-margined wing, nearly as tall as shell disc. Ventral margin curved. Posterior slope somewhat biangulate, moderately narrow, steep. Umbo not elevated above hinge line. Nacre iridescent anteriorly, bluish white, salmon or brown towards umbo, opaque, strong striations. Left valve with two lateral teeth, diverging, textured. Left valve with one large, oblique pseudocardinal tooth extending from umbo to anterior adductor muscle, otherwise deeply fractured surface dentition. Right valve with one lateral tooth, slightly curved, textured. Right valve with two oblique pseudocardinals extending from umbo to adductor muscle (in smaller individuals), posterior pseudocardinal is modified to deeply fractured surface with multiple oblique ridges. Supraanal aperture greater than $5 \times$ longer than pallial fusion between excurrent and supra-anal, smooth, tall. Excurrent aperture smooth, shorter than incurrent. Incurrent with 1 or 2 rows of short, conical-shaped papillae. Perforated septa, connections much smaller than perforations. Ectobranchous brooding.

Distribution

Restricted to the Mun watershed (Mekong drainage) in eastern Thailand (Fig. 36).

Laterally swollen and cream-coloured with brooding egg.

Ecoregion

Khorat Plateau.

Hyriopsis sakhonensis, sp. nov.

(Tables 1, 3; Fig. 1, 9, 27, 33, 36; Tables S1, S2; Fig. S1–S5)

Type locality

Songkhram River, near confluence with Un River at bridge N of Ban Si Songkhram, Nakhon Phanom Province, Thailand, 17.63400, 104.24600.

Types

Holotype, UF 564757. Paratypes, UF 507786 (n = 6), same locality data as the holotype.

Material examined

8 lots (Table S1).

Diagnosis

Hyriopsis sakhonensis is morphologically very similar to *H. phuphaniensis* and *H. kratiensis* but tends to have a more bluntly pointed posterior end.

Description

Shell elongate with large posterior wing, small anterior wing, thick shelled. Anterior end slightly sinuous to slightly rounded. Posterior end pointed. Dorsal margin consists of large smoothmargined wing, nearly as tall as shell disc. Ventral margin curved. Posterior slope gentle, slightly biangulate. Umbo not elevated above hinge line. Nacre iridescent anteriorly, bluish or purplish white, salmon or pink towards umbo, opaque, strong striations. Left valve with two lateral teeth, straight, diverging, textured. Left valve with one small, oblique pseudocardinal tooth extending from umbo to anterior adductor muscle, otherwise a series of shallow ridges. Right valve with one lateral tooth, straight, textured. Right valve with two oblique pseudocardinals extending from umbo to adductor muscle, many shallow ridges posterior to teeth. Supra-anal aperture greater than $5 \times$ longer than pallial fusion between excurrent and supra-anal, smooth, tall. Excurrent aperture smooth, shorter than incurrent. Incurrent with 1 or 2 rows of short, conical-shaped papillae. Perforated septa, connections slightly smaller than perforations. Ectobranchous brooding. Limited lateral swelling and creamcoloured when brooding eggs.

Distribution

Restricted to the Songkhram watershed (Mekong drainage) in eastern Thailand (Fig. 36).



Fig. 36. Dot distribution map of Hyriopsis phuphaniensis, H. sakhonensis, H. khoratensis and H. kratiensis.

Ecoregion

Khorat Plateau.

Hyriopsis undescribed

(Table 1; Fig. 1, 27, 35; Tables S1, S2)

Taxonomic opinions since Haas (1969a)

Hyriopsis sp. 1. – Zieritz *et al.* (2016, appendix S2), Bolotov *et al.* (2017*a*, p. 14, table S1; 2017*b*, table S1), Konopleva *et al.* (2019*a*, table S1; 2019*b*, appendix 1), Huang *et al.* (2019, table S4), Bolotov *et al.* (2020, table S1).

Hyriopsis bialatus [in part] – Muanta *et al.* (2019, table S1). *Hyriopsis* sp. – Zieritz *et al.* (2020, p. 2243).

Material examined 10 lots (Table S1).

Diagnosis Not available. Shell characters very similar to *H. bialata*.

Distribution Chao Phraya drainage in southern Thailand (Fig. 35).

Ecoregion Chao Phraya.

Remarks

This undescribed species has been consistently recovered as a divergent molecular lineage in comparison to all other recognised *Hyriopsis* species. However, we have neither collected this species nor could we locate any voucher specimens with soft anatomy, and therefore choose not to describe it.

Hyriopsis velthuizeni (Schepman, 1896)

(Table 1; Fig. 1, 33; Table S1)

Unio velthuizeni Schepman, 1896, p. 160, pl. 4, fig. 1–1a.c. *Type locality*:
'Mandai River near Nanga Kalis' [Mandai River, near Nanga Kalis, West Kalimantan Provine, Borneo Indonesia, 0.69092, 112.91016]. *Type(s)*: syntypes, RMNH.MOL.337637 (n = 1); ZMA.MOLL.139244 (n = 1), both in the Naturalis Biodiversity Center, Leiden.

Taxonomic opinions since Haas (1969a)

Hyriopsis velthuizeni – Haas (1969*a*, p. 147), Graf and Cummings (2007, p. 310), Zieritz *et al.* (2018*a*, online table 1), Zieritz *et al.* (2020, p. 2237).

Material examined

3 lots (Table S1).

Diagnosis

Hyriopsis velthuizeni is unlike all other *Hyriopsis* in that its posterior wing, umbo, and anterior wing form a straight line.

Distribution

Sumatra and Borneo.

Ecoregion

Kapuas.

Remarks

Geographic information available for this species is limited but suggests an unusual distribution. Of the three records we were able to examine and digitise, none could be georeferenced, and, as such, a dot distribution map could not be generated. The type locality of *Unio velthuizeni*, Mandai River near Nanga Kalis, can be georeferenced [0.69092, 112.91016] but the type specimens were unknown to us until just before publication and were not included in our Material Examined.

No other species of the Contradentini or Rectidentini is thought to be distributed on Borneo and Sumatra but absent from Java. This unusual distribution may be explained by the Paleo-North Sunda River which is thought to be a historical hydrological connection between these two modern landmasses (Voris 2000), but more carefully delineated species boundaries are necessary to test this hypothesis. The species has not yet been included in a molecular phylogeny.

Genus Prohyriopsis Haas, 1914

Prohyriopsis Haas, 1914: 76. Type species: Unio stolatus von Martens, 1900 by original designation.

Diagnosis

Distinguished from *Hyriopsis* by a smaller wing and the presence of sculpturing on the posterior slope.

Distribution

Central Sumatra.

Species

We recognise one species in the genus Prohyriopsis (Fig. 26).

• Prohyriopsis stolata (von Martens, 1900).

Remarks

This taxon is known from a single specimen, the holotype of *Unio stolatus* von Martens, 1900 (ZMB 51795).

Prohyriopsis stolata (von Martens, 1900)

(Table 1; Fig. 1, 10, 26, 34; Table S1)

Unio stolatus von Martens, 1900, p. 15. Type locality: 'See Danau Bura, Indragiri' [Indragiri River, Danau Baru, Riau Province, Sumatra, Indonesia, -0.33196, 102.40482]. Type(s): holotype, ZMB 51795.

Taxonomic opinions since Haas (1969a)

Prohyriopsis stolata – Haas (1969a, p. 108; 1969b, N431, fig. D29:7), Graf and Cummings (2007, p. 311), Zieritz et al. (2018a, online table 1).

Material examined

1 lot (Table S1).

Diagnosis

Same as for genus.

Distribution

Known only from the type locality in Indragiri drainage in central Sumatra (Fig. 34).

Ecoregion

Southern Central Sumatra.

Remarks

The species has not yet been included in a molecular phylogeny.

Undetermined taxa

'Contradens fultoni' Haas, 1930

Contradens semmelincki fultoni Haas, 1930, p., fig. 8. Type locality: 'Manson, Tonkin' [Mau Sơn, Lộc Bình District, Lạng Sơn, Vietnam]. Type(s): holotype, SMF 3735 by original designation.

Taxonomic opinions since Haas (1969a)

Contradens semmelinki fultoni Haas, 1930 – Lopes-Lima et al. (2017, p. 177).

Contradens fultoni Haas, 1939 [sic] - Do et al. (2018, p. 5).

Diagnosis

NA.



Fig. 37. Correlation of fish and mussel diversity across the freshwater ecoregions of South-east Asia.

Distribution

Disjunct distribution in northern Vietnam. Known from two records: SMF 3735 – 1 valve from Manson, Tonkin; NCSM 84934 – 2 specimens from Phong Tho, Vietnam.

Ecoregions

Xi Yiang, Hong Song.

Drainages

Zhujiang [Pearl River], Hong Song [Red River].

Remarks

The validity and systematic position of this species are uncertain and may have important implications if it belongs to the Contradentini as some of its morphological characters suggest. If the species is valid and belongs among the Contradentini it would be the only member of the Contradentini+Rectidentini radiation distributed east of Mekong drainage and outside of the South-east Asian subregion, and into the East Asian subregion (Fig. 7). The mussel fauna of East Asia is almost entirely different from that of South-east Asia and the presence of a member of the Contradentini in this region would be highly uncharacteristic of that regional assemblage (Zieritz *et al.* 2018*a*; Bolotov *et al.* 2020).

The type specimen of *Unio fultoni* (SMF 3735: 1 valve) is from Manson, Tonkin, which is thought to correspond to Mou Son, Vietnam (Do *et al.* 2018) – a mountainous region in north-eastern Vietnam draining the headwaters of the Pearl drainage. The single valve of the holotype does resemble members of the Contradentini, especially *Lens*, by sharing a similar shell outline, yellowish-brown periostracum with a green posterior slope, and lamellar pseudocardinal teeth nearly parallel to the lateral teeth. However, this record is geographically very distant, ~250 aerial miles from any of the confirmed Contradentini+Rectidentini records.

The other putative record of 'C'. fultoni (NCSM 84934: 2 specimens) was recently collected from the Hong Song drainage and is much closer in proximity, ~90 aerial miles, to other confirmed Contradentini records in the Mekong drainage (but is distant from the type locality). These specimens are morphologically quite similar to L. comptus and close to this species' northern range (Fig. 14). It may be that these specimens represent a disjunct population of L. comptus in the Song Hong drainage, suggesting a recent stream capture between the Mekong and Song Hong. However, other 'C'. fultoni specimens (NCSM 84935: 2 specimens) collected during this same expedition and thought to be from outside the Mekong drainage are misidentified and have an incorrect drainage assignment. This record is listed as being collected from the Ma drainage but the given latitude and longitude for this record are within the Mekong drainage (Fig. 14), and the published COI sequence from this record (KX822636, Lopes-Lima et al. 2017) is recovered within our L. comptus clade (Fig. 12). Further research is needed to determine the accuracy of the two putative 'C'. fultoni records, and validity and systematic position of that nominal species.

Undescribed Contradentini sp.

Taxonomic opinions since Haas (1969a)

Trapezoideus exolescens – Pfeiffer and Graf (2013, p. 251; 2015, p. 310), Lopes-Lima *et al.* (2017, p. 177). Trapezoideus sp. 1 – Bolotov et al. (2017a, table S1).

Physunio sp. 'Trapezoideus' – Bolotov et al. (2017b, table S1), Konopleva et al. (2019a, table S1; 2019b, appendix 1), Huang et al. (2019, table S4), Bolotov et al. (2020, table S1).

Diagnosis

NA.

Distribution

Mekong drainage in northern Laos.

Ecoregions

Upper Lancang.

Remarks

This molecular lineage is known from one sequenced specimen (UMMZ 304347: GenBank accession KP795036) from Gnot Ou, Laos and is strongly divergent from all other known Contradentini. The lineage is clearly a part of the Contradentini but its position among that tribe remains uncertain. It may represent an undescribed genus. Greater sampling of northern Laos is necessary to resolving the systematic position and taxonomic status of this undescribed lineage.

Discussion

Distribution and geographic sampling bias of the Contradentini+Rectidentini

The geographic scope of this radiation is supported by 1837 digitised and imaged records from 15 natural history collections (Fig. 1, 2, Table S1, images available at http:// www.mussel-project.net/). These data allowed us to more rigorously determine the distribution of each taxon but also provided a means to understand geographic sampling bias, which can be useful in determining where future sampling will be especially useful. The Contradentini+Rectidentini is distributed across much of South-east Asia from the Irrawaddy drainage in the west, to the Mekong drainage in the east, and south across the Malay Peninsula and throughout much of the Malay Archipelago, including the islands of Sumatra, Java, Borneo and Palawan.

The examined material is unevenly distributed across the 19 freshwater ecoregions occupied by the Contradentini +Rectidentini (Fig. 3). Our understanding of the total geographic distribution of this clade would benefit from greater sampling focused on less completely characterised regions. This is especially true of the northern ecoregions of the Mekong drainage, the ecoregions east of the Mekong, the ecoregions of the Salween drainage and the ecoregions to the west of the Salween, and the ecoregions of the Malay Archipelago. We take this opportunity to highlight and briefly discuss each of these poorly characterised regions.

Sampling efforts within the Mekong drainage have been strongly biased towards its southern half (Fig. 2). For example, we identified 374 museum records from the Khorat Plateau but documented only 23 records from the neighbouring upstream ecoregion, the Lower Lancang, and recorded zero lots from the ecoregion upstream of that, the Upper Lancang ecoregion (Fig. 3). The Upper Lancang and Lower Lancang ecoregions are more mountainous than the southernly ecoregions (Fig. 2), and the availability of suitable mussel habitat and access to sample that habitat appear to be driving the lack of material from this region. The paucity of records from the northern half of the most species-rich drainage in South-east Asia (Table 2) is likely to result in the underestimation of species richness in this biodiversity hotspot. Future sampling efforts focused on the more mountainous regions of the Mekong drainage should be a priority.

The ecoregions east of the Mekong drainage are also poorly sampled and this is an important area for future research. The lack of Contradentini or Rectidentini records in the Southern Annam ecoregion of central and southern Vietnam is somewhat surprising (Fig. 7). This ecoregion is separated from the Mekong by a relatively small drainage divide, and at least one other South-east Asian freshwater mussel radiation, the Pseudodontini, has dispersed into this ecoregion (e.g. UMMZ 108074, NHMUK 1901-12-12-98). The limited number of museum records from this ecoregion complicates delimiting the south-eastern distribution of the Contradentini+Rectidentini, and additional field and museum sampling effort in the region should also be a research priority. The unknown systematic position, validity, and geographic range of north Vietnamese nominal species 'Contradens' fultoni also obscures delimiting the Contradentini +Rectidentini north-eastern range (see 'Contradens' fultoni account). It remains unclear if the apparent absence of the Contradentini+Rectidentini in the non-Mekong ecoregions of Vietnam (Song Hong, Northern Annam, and Southern Annam ecoregions) is real or perceived. Greater sampling effort in these ecoregions would more completely elucidate the geographic extent of this radiation and the biogeographic barriers in the region more generally (e.g. the divide between the South-east Asian Subregion and the East Asian Subregion, Fig. 7).

The Salween ecoregion and the ecoregions to the west tend to have fewer Contradentini+Rectidentini records in comparison to most other ecoregions in mainland Southeast Asia (Fig. 2, 3). While our knowledge of mussel diversity in these regions has grown dramatically in just the past few years (Bolotov et al. 2017a, 2019b, 2020; Konopleva et al. 2019a), evidence for the geographic extent of this diversity remains quite limited. Of the 13 Contradentini +Rectidentini species found in the Salween River ecoregions and the ecoregions to the west, over half are known from just their type localities. Similar to the sampling biases in the Mekong River, the upper Salween is also poorly sampled and there are no known Contradentini records from the Upper Salween ecoregion (Fig. 7). The Lower & Middle Salween ecoregion extends further south than the biogeographic divide recently proposed by Bolotov et al. (2020), who found convincing evidence for a significant faunal break at the Tanintharyi-Lenya drainage divide. This appears to be an area where fish and mussel biogeographic patterns may differ but further sampling of southern extent of the Lower & Middle Salween ecoregion is also needed (Bolotov et al. 2020).

The distribution and diversity of the Contradentini +Rectidentini of Sundaland are poorly characterised in comparison to that of mainland South-east Asia (Fig. 3). However, there has been much recent progress in sampling the Malay Peninsula and parts of the Malay Archipelago (Zieritz et al. 2016, 2018b, 2020). We know of no records of the Contradentini+Rectidentini from several of the archipelago's southern ecoregions including Ache, Indian Ocean Slope of Sumatra and Java, Borneo Highlands, and Eastern Borneo (Fig. 7). These regions have been poorly sampled for freshwater mussels and deserve further attention. Data from these ecoregions will be useful for testing alternative hypotheses regarding the various hypothesised palaeo-drainages in Sundaland (e.g. Paleo-Malacca Straits River, Paleo-North Sunda River, Paleo-East Sunda River - see discussion below).

Individually, the two tribes have quite similar geographic distributions. The Contradentini and the Rectidentini co-occur across all of South-east Asia except the Rectidentini is absent from three ecoregions occupied by the Contradentini (Fig. 3). The Contradentini is quite diverse in the Salween and Sittaung–Irrawaddy ecoregions, whereas the Rectidentini is absent from them (Table 2). The only other area in which the Contradentini occurs but the Rectidentini does not is the island of Palawan. However, only one freshwater mussel species, *Pressidens exanthematicus*, occurs on Palawan and the systematic position of this taxon remains untested. We tentatively maintain it among the Contradentini (Pfeiffer *et al.* 2019).

Diversity and Endemism in the Contradentini and Rectidentini

The Contradentini and Rectidentini have their greatest species richness in the Mekong drainage with 24 species in total, 11 and 13 species respectively (Table 2). The Mekong is also the drainage with the greatest endemism: 19 of the 24 Contradentini+Rectidentini species in the Mekong are endemic to portions of that drainage (especially the Khorat Plateau – discussed below). The next most species-rich drainage, the adjacent Chao Phraya, is less than half as rich as the Mekong, with just 10 Contradentini+Rectidentini species (Table 2). The Contradentini typically has greater species richness than the Rectidentini in the drainages and ecoregions of mainland South-east Asia (the Mekong being the exception), whereas the Rectidentini tends to be slightly more diverse than the Contradentini in Sundaland (Table 2, Fig. 4).

Many species of the Contradentini+Rectidentini were historically thought to be geographically widespread and distributed across several of South-east Asia's large drainages (e.g. Brandt 1974; Zieritz *et al.* 2018*a*). However, this paradigm has been recently questioned in favour of the hypothesis that most of the geographically widespread species are instead species complexes composed of several singledrainage-endemic species (Bolotov *et al.* 2017*a*). Our analysis demonstrates that the level of drainage-specific endemism in the Contradentini+Rectidentini has been recently overstated, as has also been shown for the Indochinellini (Pfeiffer *et al.* 2018*a*). All 24 Contradentini+Rectidentini species treated in

Bolotov et al. (2017a) were considered to be endemic to single drainages (their supplementary table 5), while more geographically comprehensive sampling shows that eight of those species are found in at least two drainages. Of the Contradentini+Rectidentini species treated in our 54 assessment, 14 are distributed in more than one drainage (Fig. 5). This recent overestimation of drainage-specific endemism appears to be an over-reliance on geographically coarse recent sampling, narrowly defined phylogenetic species, and a lack of focus on historical sampling. More completely leveraging the publicly available data in the world's natural history museums provides a more detailed view of South-east Asian freshwater mussel biogeography and one that more accurately reflects the dynamic geoclimatic history of the region.

Conversely, our assessment of the Contradentini +Rectidentini in the Irrawaddy, Sittaung and Salween does show very high levels of endemicity, similar to the levels proposed by Bolotov et al. (2017a). Twelve of the 13 Contradentini species in these three drainages are endemic to a single drainage, Lens contradens being the only exception. The high levels of endemism in the Irrawaddy, Sittaung and Salween are distinctly different from most other parts of South-east Asia, except for perhaps the Mekong and Borneo (Table 2). That said, the taxa thought to be endemic to the Irrawaddy, Sittaung and Salween are known from comparatively fewer records (Fig. 1) and these regions are more poorly sampled in comparison to the rest of mainland South-east Asia (Fig. 2, 3). As the sampling increases in the region we may see this level of endemism decrease, as has been the case with the other more completely sampled parts of South-east Asia (Pfeiffer et al. 2018a; this study).

Diversity and distribution patterns of the Contradentini +Rectidentini

As we revised the diversity and distribution of this radiation several interesting biogeographic patterns emerged.

Multiple Mekong radiations

We recovered four independent multispecies radiations endemic to the Mekong drainage (Fig. 9). These four radiations are distributed across the phylogeny of the Contradentini+Rectidentini and include at least 16 species, with many of these species being restricted to small portions of the Khorat Plateau ecoregion. Two of these Mekong radiations are in the Contradentini – a six-species clade in Lens (Fig. 12, 13, 14), and a 2-4-species clade in Physunio (Fig. 18, 19). The other two Mekong radiations are in the Rectidentini - a 4-species clade in *Ensidens* (Fig. 30, 32), and a 4-species clade in Hyriopsis (Fig. 27, 36). While the morphological diversification in these Mekong radiations is very limited (e.g. see the 'diagnoses' in our taxonomic accounts), they are molecularly quite divergent. And perhaps most convincingly to their recognition as biological species, is that these morphologically conserved and molecularly divergent lineages occur in the same drainage, and often occur sympatrically with their sister taxon, suggesting that these species are intrinsically reproductively isolated.

In each of these independent Mekong radiations, there are consistent biogeographic patterns that suggest the presence of several significant barriers to dispersal within the modern-day Mekong drainage, most of which are in the Khorat Plateau ecoregion. Within these Mekong radiations we recovered several species-level clades that are largely endemic to the Mun watershed (Ensidens sagittarius, Hyriopsis khoratensis, Lens pallegoixi), the Songkhram watershed (Ensidens dugasti, Hyriopsis sakhonensis, Physunio modelli Songkhram clade, Lens maenamensis Songkhram clade), and, to a lesser extent, the longitudinal portion of the middle Mekong (Ensidens spiculus, Lens rolfbrandti). This specific and consistent biogeographic pattern in the Khorat Plateau suggests that there are several significant biogeographic barriers within the Mekong drainage that are driving a substantial portion of diversification in the Contradentini+Rectidentini. Our ability to detect these finer-scale biogeographic patterns may be because the Khorat Plateau is the most well sampled portion of the Mekong drainage (Fig. 3). Some of these apparent barriers within the Mekong drainage have also been observed in the Indochinellini (Kongim et al. 2015; Pfeiffer et al. 2018a). We suspect that increased sampling in other major watersheds of the Mekong may reveal additional intradrainage barriers to dispersal (e.g. Tonle Sap, Stung Treng, Xe Don, Nam Ou).

It is also worth noting that each of these Mekong radiations contain species that are commonly found in, or close to, the Mekong River proper (i.e. L. comptus, E. jaculus, H. phuphaniensis, P. pellucidus), suggesting that these taxa may be closely associated with the Mekong River mainstem ecosystem. Several taxa in the North American mussel assemblage are associated with large river ecology and are commonly referred to as 'large-river specialists' (Haag 2012). Although very little is known about the ecology of these Mekong River species, their large distributions and limited genetic divergences are reminiscent of other well known large river specialists in North America (Berg et al. 2007; Roe and Boyer 2015; Pfeiffer et al. 2018b). Our understanding of how ecology shapes the diversity and distribution of South-east Asian freshwater mussels is almost non-existent, and, as a consequence, the observed biogeographic patterns in Southeast Asian freshwater mussels are often explained by geophysical phenomena alone (including those discussed here). It remains unclear how ecology shapes freshwater mussel diversity and distribution in South-east Asia.

Stream capture

We have documented how many Contradentini+Rectidentini species are distributed across multiple drainages, and it is worthwhile to speculate how these disjunctions may have been precipitated. Many of these disjunctions are likely the product of two different geoclimatic phenomena – stream capture and historical confluence. Stream capture is when a drainage divide migrates and causes a portion of one drainage to be redirected (victim) and integrated into an adjacent drainage (aggressor) (Willett *et al.* 2014). Historical confluence is when two adjacent drainages, separated by a marine ecosystem, become a single larger palaeo-connected drainage as sea level drops and the rivers converge on the recently exposed continental shelf (Dias *et al.* 2014).

Several species of the Contradentini+Rectidentini have disjunct distributions that may be best explained by stream capture and geodispersal. For example, Lens contradens is nearly absent from the Mekong drainage but occurs in three, isolated, low-order streams, very near the Mekong-Chao Phraya drainage divide - the Kok, Ing and Loei watersheds (Fig. 15). The absence of intervening L. contradens records from the Mekong River is consistent with these peripheral populations being integrated into the Mekong system by multiple separate stream-capture events, rather than one isolated event. However as noted before, this region of the Mekong is undersampled and further sampling efforts are needed to determine whether these populations are as isolated as the currently available data suggest. All three of these rivers (Kok, Ing, Loei) have been previously implicated in hypothesised connections between the Mekong and Chao Phraya (Hutchison 1989; Rainboth et al. 2012), and this part of the Mekong has many sharp changes in channel direction, a highly crenulated drainage divide, and many obtuse conflunce angles - each of which are common network geometries of drainage rearrangements (Bishop 1995).

Similarly, Lens contradens is absent from the Salween River except for one relatively small watershed, the Moei, very near the Salween-Chao Phraya-Mae Klong drainage divide (Fig. 15). This disjunct population of L. contradens in the Salween suggests a stream-capture event caused part of the Mae Klong or Chao Phraya to start draining to the Salween. Bohlen et al. (2020a, 2020b) hypothesised that the Salween drainage recently captured part of the Mae Klong drainage ~1.5 million years ago and that this event effected the distribution of at least two freshwater fish species. These putative stream-capture events occur in relatively small, high-gradient watersheds very near a drainage divide, which are likely areas of drainage rearrangement especially 'bottom up' processes such as headwater extension (Bishop 1995). These watersheds (Moei, Kok, Ing, Loei) also tend to flow in a northerly direction, opposite the general direction of the Mekong and Salween River mainstems, creating strongly obtuse confluences that are also characteristic of drainage rearrangements (Bishop 1995).

We also found disjunct distributions in two species of Ensidens that also suggest stream capture. Ensidens ingallsianus is distributed across much of eastern Indochina but the species is known only from the Mekong drainage by two isolated populations very close to the Mekong-Chao Phraya-Bang Pakong drainage divide at the south-western edge of the Khorat Plateau (Fig. 31). This disjunction and the shallow molecular divergence suggests that the Mekong drainage recently captured portions of the Chao Phraya or Bang Pakong, or perhaps both. The western edge of the Khorat Plateau is a geologically active area that is thought to have caused many minor and major stream-capture events between the Mekong and the Chao Phraya. Although the timings of these capture events are often poorly understood, the majority appear to have occurred in the Quaternary (Hutchison 1989; Heggemann et al. 1994; Parry 1996; Rainboth et al. 2012), which may be consistent with shallow

genetic divergences observed here. *Ensidens telus* shows a somewhat inverse pattern, being distributed across much of the lower Mekong with disjunct populations in the eastern Bang Pakong drainage, suggesting that the Bang Pakong recently captured parts of the Mekong drainage. The drainage divide between these two watersheds is much less dramatic than in comparison to the other hypothesised captures (Fig. 31) and there is evidence of hydrological connectivity between the Bang Pakong and Tonle Sap (Rainboth 1996; Rainboth *et al.* 2012).

Evidence also exists for at least one intradrainage stream capture in the Mekong – where a portion of the Mun watershed (Khorat Plateau ecoregion) was captured by the Loei watershed (Lower Lancang ecoregion). This putative stream capture is supported by the distribution and genetic structure of *P. modelli* (Fig. 18, 19). We found a shallow clade of *P. modelli* that is largely restricted to the Khorat Plateau and Kratie–Stung Treng ecoregions; however, individuals from the Loei watershed, are nested deeply within this clade. *Physunio modelli* is otherwise absent from the Lower Lancang drainage and the northern portion of the Khorat Plateau. This disjunction is best explained by the Loei watershed.

The disjunct distributions of these species and the geomorphology of the watersheds have many characteristics of geodispersal via stream capture, but these biogeographic hypotheses deserve further scrutiny. Too often have disjunct distributions and drainage network morphologies (e.g. capture elbows, obtuse confluence angles, crenulated drainage divides) been used as evidence of drainage rearrangement and faunal exchange without direct geological evidence (Bishop 1995) – those described here are no exception. Ideally, hypotheses of drainage rearrangement should be supported with dated geological evidence that can be demonstrably linked to palaeodrainage (Bishop 1995; Fan *et al.* 2018).

Historical confluence

During the last glacial maximum, much of the world's freshwater was tied up in glaciers, which dramatically lowered global sea levels and converted many of the world's shallow seas to large coastal plains. This geoclimatic phenomenon profoundly shaped global freshwater biodiversity as these lower sea-level stands created many palaeo-connected river systems that facilitated dispersal of many obligate freshwater taxa (Dias et al. 2014). In South-east Asia, this phenomenon exposed the entirety of the Sunda Shelf and this new landmass was drained by several great palaeo-drainages, the largest of which was the Paleo-Siam River system (Voris 2000). Today much of the Paleo-Siam River is 'drowned' and separated into various independent drainages including the Chao Phraya, Mae Klong, Bang Pakong, Chantaburi, and many smaller coastal drainages of the Malay Peninsula. The palaeo-connections between these modern drainages have shaped freshwater biodiversity in South-east Asia (de Bruyn et al. 2013; Dias et al. 2014) and are reflected in the distribution of many Contradentini and Rectidentini.

Several Contradentini+Rectidentini species are distributed across many independent drainages but have very limited genetic divergences. This geographic and genetic pattern is consistent with recent dispersal and connectivity associated with the Paleo-Siam River system and is found in many species, including Lens contradens (Fig.12, 15), Lens inornatus (Fig. 12, 16), Physunio superbus (Fig. 18, 19), Trapezoideus foliaceus, T. subviridus, Solenaia emarginata (Fig. 18, 22), Ensidens. ingallsianus (Fig. 30, 31), Hyriopsis myersiana (Fig. 27, 34), and H. desowitzi (Fig. 27, 35). The phylogeographic patterns of these taxa indicate that there is considerable variation within the degree of connectivity or isolation within the Paleo-Siam River system - some taxa are distributed across much of the palaeo-connected system (E. ingallsianus, L. contradens, P. superbus) whereas others are restricted to much smaller portions of the greater palaeodrainage (H. myersiana, T. foliaceus, T. subviridis). Clearly, there is an abundance of evidence suggesting that the Paleo-Siam River system has shaped Contradentini +Rectidentini diversity and distribution.

However, the importance of the other hypothesised palaeodrainages in the region (e.g. Paleo-Malacca Straits River, Paleo-North Sunda River, Paleo-East Sunda River, Voris 2000) in shaping Contradentini+Rectidentini diversity and distribution is very limited. Lens contradens specimens collected from areas implicated in the Paleo-Siam River (e. g. Malay Peninsula eastern slope) and areas of the Paleo-Malacca River (e.g. Malay Peninsula western slope) show some limited sequence divergence that may reflect a pattern consistent with the influence of the Paleo-Malacca River (Fig. 12). Rectidens sumatrensis also shows some limited molecular divergence consistent with separation between the Paleo-Malacca River and the palaeo-drainages of northern Borneo (Fig. 27). The unusual geographic distribution of Hyriopsis velthuizeni may be consistent with the existence of the palaeo-North Sunda River system but the boundaries and validity of this putative species are too poor to make any meaningful inferences. Increased sampling of the Malay Archipelago will be necessary to better understand how palaeo-drainage evolution has affected freshwater mussel diversity and distribution in the region.

Zoogeographic regions

Several recent papers have delimited, refined and discussed various useful freshwater mussel zoogeographic regions in South-east Asia (Graf and Cummings 2007; Zieritz *et al.* 2018*a*; Konopleva *et al.* 2019*a*; Bolotov *et al.* 2020). However, these regions have been somewhat subjectively defined rather than relying on analysis of the underlying distributional data. Our UPGMA analysis of Contradentini +Rectidentini presence or absence across the freshwater ecoregions of South-east Asia is consistent with recognising six zoogeographic regions (Fig. 7*a*) and our MNDS analysis of Contradentini+Rectidentini phylogenetic diversity recovers a similar biogeographic pattern, consistent with recognising five (or six) cohesive zoogeographic provinces (Fig. 7*b*). For the most part, these regions (Graf and Cummings 2007; Zieritz

et al. 2018*a*; Konopleva *et al.* 2019*a*; Bolotov *et al.* 2020), but provide more objectivity. We briefly discuss each of these provinces with respect to the diversity of the Contradentini and Rectidentini, and hope that it is useful in understanding biogeographic patterns in South-east Asian freshwater biodiversity more generally.

The Western Indochina province is the Sittaung-Irrawaddy ecoregion and is the only mussel province in South-east Asia where the Contradentini occurs but the Rectidentini does not. The absence of the Rectidentini causes these drainages to be the least phylogenetically diverse in our assessment (Table 2). Despite these two drainages sharing geographically close river mouths and having several natural interbasin connections, these systems are thought to be composed of entirely endemic Contradentini assemblages. This level of drainage-specific endemism is unlike the diversity patterns for the rest of South-east Asia (Table 2) but is consistent with the hypothesis that at least the Irrawaddy is thought to be a palaeo-disconnected drainage (Dias et al. 2014 - although Sittaung River not treated in their analysis). It remains unclear whether the level of Contradentini+Rectidentini endemism in these two adjacent drainages is real or an artefact of the paucity of records from this ecoregion and its taxa (Fig. 1, 3).

The Salween province is composed of the Upper Salween, Inle Lake, and Lower & Middle Salween ecoregions. This province appears to represent a transitionary zone between Western Indochina and the Gulf of Thailand provinces. The Salween province shares one genus of the Contradentini +Rectidentini in common with the Western Indochina (Yaukthwa) and two with the Gulf of Thailand province (Lens and Trapezoideus) and this fact strongly influences our UPGMA analysis (Fig. 7a). However, the observed phylogenetic diversity of the Salween drainage is much more similar to the drainages of Western Indochina province than it is to the drainages of the Gulf of Thailand provinces (Fig. 7b). This disparate pattern led us to classify this region as distinct from the adjacent provinces and to highlight its transitionary nature, at least with respect to the Contradentini+Rectidentini. Bolotov et al. (2020) demonstrated that there is a substantial change in freshwater mussel fauna at the Tanintharyi-Lenva drainage divide, whereas the Salween ecoregion extends much further south. This disparity may suggest that mussel and fish zoogeographic barriers in area are incongruent or the ecoregion may be in need of refinement.

The Mae Klong, Chao Phraya, and Eastern Gulf Thailand ecoregions comprise the Gulf of Thailand province. This region has quite high species and phylogenetic diversity but very low drainage-specific endemism (Table 2). The similarity in the mussel assemblages of these three ecoregions is likely a product of the historical confluences between the Mae Klong, Chao Phraya, Bang Pakong, Chantaburi, and smaller coastal drainages of the Malay Peninsula associated with the Paleo-Siam River. The Gulf of Thailand province is also faunistically similar to the South-western Sundaland province (Fig. 7); a shared similarity in these assemblages is also likely to be partially explained by the Paleo-Siam River. The Mekong province is composed of the Upper Lancang, Lower Lancang, Khorat Plateau, Kratie–Stung Treng, and Mekong Delta ecoregions. While the diversity varies substantially among ecoregions (Fig. 4), collectively they form a cohesive zoogeographic area (Fig. 7*a*). For example, the Lower Lancang and Mekong Delta ecoregions have similar species richness (six and seven species respectively), but only two species are shared between them (i.e. *Lens comptus* and *Physunio modelli*). Clearly, there are several influential biogeographic barriers within this drainage, and the currently recognised ecoregions appear to do a good job at characterising these intradrainage assemblages.

The South-western Sundaland province includes the Malay Peninsula Eastern Slope, North Central Sumatra-Western Malaysia, Ache, Southern Central Sumatra, Indian Ocean Slope of Sumatra and Java, Southern Sumatra-Western Java, and Central and Eastern Java ecoregions. The Contradentini+Rectidentini fauna of this region is most similar to the Gulf of Thailand assemblage but also shares some taxa with the Bornean province. The northern extent of this province is somewhat consistent with a long recognised and well known zoogeographic transitionary zone between the Indochinese and Sundaland regions which occurs more or less near the Isthmus of Kra (Wallace 1876; Woodruff and Turner 2009), although the latitude of this boundary and how it was generated is thought to be highly taxon dependent (Lohman et al. 2011; Dejtaradol et al. 2016). Several freshwater taxa in the region have biogeographic patterns that are thought to be limited by three prominent marine transgressions (i.e. Isthmus of Kra seaway, Surat Thani-Krabi seaway, Kangar-Pattani seaway) that inundated parts of the Malay Peninsula during the Pliocene (mussel, Bolotov et al. 2020; snail, Veeravechsukij et al. 2018; prawn, de Bruyn et al. 2005; fish, Bohlen et al. 2020a). However, these historical seaways appear to have had limited effect on the modern-day distribution or genetic structure of any of the taxa analysed here - except for perhaps Trapezoideus lenva but that species is known only from its type locality. Most freshwater mussels that occur on or near the Malay Peninsula have ranges that terminate well north (Lens inornatus, Trapezoideus foliaceus, Hyriopsis myersiana) or well south (Rectidens sumatrensis) of the Isthmus of Kra. And four of the analysed taxa have populations on both sides of the Isthmus of Kra that show very limited genetic differentiation (Lens contradens, Physunio superbus, Ensidens ingallsianus, Hyriopsis bialata). It is likely that these taxa dispersed south after global sea levels decreased and the marine transgressions near the Isthmus of Kra were replaced by coastal plain and the growing Paleo-Siam River.

The Borneo province includes the Kapuas, North-western Borneo, Borneo Highlands, South-eastern Borneo, Northeastern Borneo, Eastern Borneo, and Palawan–Busuanga– Mindoro ecoregions. This region is distinct from the neighbouring South-western Sundaland province in terms of its species assemblage and phylogenetic diversity (Fig. 7). Despite including only a small fraction of the Bornean assemblage in our analysis of phylogenetic β diversity, this province is phylogenetically divergent from all others in the South-east Asian Subregion. The high level of phylogenetic diversity in this province is consistent with the divergent morphologies of many of its taxa and their widespread taxonomic distribution (Pfeiffer *et al.* 2019).

These provinces provide a useful step towards more objectively defining freshwater mussel regional assemblages in South-east Asia, but increasing the hydrographic resolution of the units would be useful. The previously defined ecoregions are practical in that they provide a unified zoogeographic framework for comparing biodiversity patterns across many freshwater assemblages, even if the ecoregions lack the more fine-scale resolution of other available hydrographic units (e.g. hydrosheds). For example, by leveraging the available freshwater ecoregions and their previously determined fish species richness (Abell et al. 2008), we can see that freshwater mussel species richness and fish species richness is strongly correlated across the ecoregions of Southeast Asia (Fig. 37). These broader taxonomic comparisons are useful in identifying freshwater biodiversity hotspots (e.g. high fish and mussel diversity in the Khorat Plateau) or identifying taxa that do not follow regional patterns of diversity (e.g. low mussel diversity in several ecoregions of the Western Sundaland Province relative to fish diversity). That said, some of the previously defined ecoregions (e.g. Lower and middle Salween) may not accurately reflect some important freshwater mussel barriers (e.g. Tanintharyi-Lenya drainage divide, Bolotov et al. 2020). We look forward to more taxonomically comprehensive and geographically nuanced evaluations of South-east Asian freshwater biodiversity.

Conclusion

Recent efforts to better understand the systematics and biogeography of the South-east Asian freshwater mussels have relied heavily on either museum specimens or recently sequenced individuals. While both of these approaches have been tremendously useful in isolation, they are greater together than the sum of their parts. This revision unites these two approaches and provides an updated systematic and biogeographic framework that future studies can use and improve.

It is remarkable how much progress has been made recently by the freshwater mussel systematics community with respect to describing the phylogeny, distribution, and diversity of the Contradentini+Rectidentini. Despite this transformation in systematic knowledge, the basic ecological requirements of this radiation remain almost completely unknown. For example, to our knowledge host fish suitability has been assessed for only one of the 54 valid Contradentini +Rectidentini species (*Hyriopsis myersiana*, Arayawatanavij *et al.* 1992). If we are to make meaningful progress with respect to understanding South-east Asian freshwater mussel ecology, evolution and biogeography, this knowledge gap must be bridged.

Evaluating the conservation status of these taxa is also an important research priority. Many of these taxa have had no formal conservation assessment, and, given the proposed taxonomic and distributional changes, most previous assessments are in need of updating. This revision, incomplete and imperfect as it is, provides an improved framework for addressing these research priorities and many others. Equipped with clearly defined genetic and geographic species boundaries organised in a biological classification that reflects evolutionary relationships, we can more completely characterise the origin and transformation of traits, how species interact with their environment, rigorously measure changes in distribution, and better appreciate the emergent properties of South-east Asian freshwater ecosystems.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

This study was funded in part by the USA National Science Foundation: All Cypriniformes Species Inventory Project (DEB 1022720) and a Doctoral Dissertation Improvement Grant (DEB 1701901).

Acknowledgements

Deein Gridsada (Suphan Buri Inland Fisheries Research and Development Center) and Tach Phanara and So Nam (Inland Fisheries Research and Development Institute, Fisheries Administration) assisted with collection and export permits for Thailand and Cambodia respectively. Special thanks to the world's natural history museums and their staff for making biodiversity data accessible.

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Handling editor: Gonzalo Giribet