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Review Article

Follow the Footsteps of Leonardo Fea: An Example of an Integrative Revision of Freshwater Mussel Taxa Described from the Former British Burma (Myanmar)

Ivan N. Bolotov,[1,2] Ekaterina S. Konopleva,[1,2] Ilya V. Vikhrev,[1] Than Win,[3] Zau Lunn,[4,5] Nyein Chan,[4] Mikhail Yu Gofarov,[1] Alexander V. Kondakov,[1,2] Alena A. Tomilova,[1] Rajeev Pasupuleti,[6] and Nalluri V. Subba Rao[7]

[1]*N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences, Northern Dvina Emb. 23, 163069 Arkhangelsk, Russia*
[2]*Northern Arctic Federal University, Northern Dvina Emb. 17, 163002 Arkhangelsk, Russia*
[3]*Department of Zoology, Dawei University, Dawei, Tanintharyi Region, Myanmar*
[4]*Fauna & Flora International-Myanmar Programme, 34 D/9 San Yae Twin Street, Kaba Aye Pagoda Road, Bahan Township, 11201 Yangon, Myanmar*
[5]*Biology Department, University of new Brunswick, PO Box 5050, 100 Tucker Park Road, Saint John, NB, Canada E2L 4L5*
[6]*Institute of Molecular Biotechnology (IMBT), Technical University of Graz, Petersgasse 14, 8010 Graz, Austria*
[7]*Zoological Survey of India, Telangana, Bhagat Singh Nagar, Hyderabad Plot 613, India*

Correspondence should be addressed to Ekaterina S. Konopleva; es.konopleva@gmail.com

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Leonardo Fea, an Italian explorer and traveler, sampled a comprehensive collection of continental Mollusca during his travels throughout the former British Burma (currently Myanmar) in 1885-1887. Cesare Maria Tapparone-Canefri, an Italian malacologist, studied this sample and published a paper with a description of numerous terrestrial and freshwater molluscan taxa new to science. This collection was partly deposited in the Museo Civico di Storia Naturale di Genova (MSNG), Italy and the Indian Museum (ZSI: Zoological Survey of India) in Kolkata. Here, we provide a re-analysis of C.M. Tapparone-Canefri's Burmese Unionidae collection. Our study reveals that the type series of only four nominal taxa described by Tapparone-Canefri as new to science in 1889 are still available in the MSNG, i.e. *Unio rectangularis*, *U. pulcher*, *U. protensus* var. *obtusatus*, and *U. marginalis* var. *subflabellata*. The first taxon is a valid species belonging to the genus *Yaukthwa*, while *U. pulcher* and *U. protensus* var. *obtusatus* are considered here as junior synonyms of the widespread *Lamellidens generosus*, and the last nominal taxon corresponds to *L. savadiensis*. The MSNG collection also contains shell lots of *Indochinella pugio pugio*, *I. pugio paradoxa*, *Indonaia andersoniana*, *Radiatula chaudhurii*, *R. mouhoti haungthayawensis*, *Lamellidens savadiensis*, *L. generosus*, *Yaukthwa nesemanni*, and *Y. zayleymanensis*, most of which were listed in Tapparone-Canefri's work under incorrect names. We revise all the freshwater mussel taxa listed by Tapparone-Canefri based on the original descriptions, available DNA sequences, morphological data, and biogeographic evidence. A freshwater mussel from the Haungthayaw River that was identified by Tapparone-Canefri as *Unio exolescens* is described here as *Trapezoideus mitanensis* sp. nov., a fourth species in this small Contradentini genus with a restricted range. Finally, new taxonomic opinions are proposed here for *Leoparreysia tavoyensis*, *Trapezidens dolichorhynchus*, *Lamellidens generosus*, and *Lamellidens savadiensis*.

1. Introduction

First studies on freshwater mussels of the former British Burma (now Myanmar) have appeared as early as 1840s [1]. In particular, the American malacologist Augustus Addison Gould published the three earliest works with descriptions of a few unionid species from Burma [1–3]. These pioneering samples were collected and sent to him by Rev. Francis Mason, a Baptist missionary and naturalist [4]. During the period of 1860-1890s, the body of taxonomic literature on freshwater mussels of the region was increasing dramatically. Most of these historical works represent descriptions of new taxa and local faunal summaries [5–13], although Blanford [14] tried to compile the first checklist of freshwater mussels described from India, Ceylon (now Sri Lanka), and Burma.

The prominent Italian malacologist Cesare Maria Tapparone-Canefri published an extensive overview of freshwater and terrestrial molluscs of the former British Burma based on new samples collected by the Italian explorer and traveler Leonardo Fea [15]. Among other animal taxa, Fea collected a comprehensive freshwater mussel sample from six localities during his travels in 1885-1887 that was largely processed by Tapparone-Canefri [15]. Interestingly, the well-known Indian zoologist Baini Prashad criticized this work as follows: "Apparently Tapparone-Canefri had to base his work to a very great extent, if not entirely, on the incomplete published descriptions of the earlier authors and on the illustrations in the Conchologia Indica of Hanley and Theobald, for most of his identifications are incorrect, this would not have happened if he had had authentically named material for comparison. He referred all his new species to the composite genus *Unio*, and gave elaborate descriptions but did not publish any figures, his work, therefore, has been a great stumbling block in the way of all later work" ([16]: 91). We would not agree with this disapproving decision, because the morphology-based taxonomy of freshwater mussels is complicated by multiple convergences in conchological traits, and it is always difficult to develop a taxonomic system for any group of the order Unionida based on morphological features alone [17–22].

Currently, our knowledge of the freshwater mussel systematics of Myanmar was largely enriched by the range of research using an integrative taxonomic approach [17–20, 22–30]. Multiple species and several genera new to science were discovered and described, as well as broad-scale revisions of already described taxa were conducted [17, 24, 29, 30]. It was shown that Myanmar harbors a species-rich and largely endemic freshwater mussel fauna and that this region could be considered a separate freshwater biogeographic domain, i.e. the Western Indochina Subregion [17, 18]. However, many old works and corresponding museum collections are yet to be checked critically (e.g., [14–16]), although the crucial importance of these historical data can be recognized in order to better understand the range shifts and population dynamics, and, hence, to estimate the conservation status of freshwater mussels [19, 22, 31, 32].

Taking into account the concerns, outlined above, this study (1) revises all the freshwater mussel taxa listed by Tapparone-Canefri [15] based on the primary descriptions, available museum specimens, and newly collected samples from the historical localities; (2) proposes new synonymies for several conchologically variable species such as *Leoparreysia tavoyensis* (Gould, 1843), *Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889), *Lamellidens generosus* (Gould, 1847), and *L. savadiensis* (Nevill, 1877); (3) describes one freshwater mussel species new to science; and (4) discusses historical records on the market trade and commercial harvesting of freshwater mussels in the former British Burma.

2. Material and Methods

2.1. Data Sampling. The Fea collection that was used by Tapparone-Canefri [15] was partly deposited in the Museo Civico di Storia Naturale di Genova (MSNG) in Italy. We studied the MSNG collection but were unable to locate many shell lots that were mentioned by Tapparone-Canefri [15]. These lots were apparently transferred to the Indian Museum (ZSI: Zoological Survey of India) in Calcutta (now Kolkata) on the request of Baini Prashad. In the revision of Burmese Unionidae, Prashad ([16]: 92) noted that "…I found that it was quite impossible adequately to work out the Burmese forms without an examination of Tapparone-Canefri's type-specimens, and I applied to Dr. R. Gestro of the Genoa Museum. He was not only kind enough sent me the whole of Fea's Burmese collection on loan, but also generously presented to the Indian Museum specimens of a number of the species, duplicates of which were still available. This kindness on Dr. Gestro's part, for which I am greatly indebted to him, has made it possible for me to assign T.-Canefri's species to their proper generic and specific position". We were able to find and check several lots from the Fea collection in ZSI under the framework of the present study.

We studied lots of freshwater mussels from Myanmar in the following museum collections: MNHN: Muséum national d'histoire naturelle, Paris, France; MSNG: Museo Civico di Storia Naturale di Genova, Genova, Italy; MCZ: Museum of Comparative Zoology, Cambridge, USA; NCSM: North Carolina Museum of Natural Sciences, Raleigh, USA; RMBH: Russian Museum of Biodiversity Hotspots, Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences, Arkhangelsk, Russia; SMF: Senckenberg Museum Frankfurt, Frankfurt, Germany; ZSI: Zoological Survey of India, Kolkata, India. Additionally, the MUSSEL Project (MUSSELp) Database (http://mussel-project.uwsp.edu) was widely used as a comprehensive source of various taxonomic information on freshwater mussels [26, 33].

New samples of freshwater mussels were collected from all the historical localities listed by Tapparone-Canefri [15] (Figure 1 and Table 1), including topotypes of several nominal taxa and a sample of a species new to science.

2.2. Morphological Studies. Comparative conchiological analyses were carried out applying differences of the shell shape, hinge plate, umbo position, muscle attachment scars,

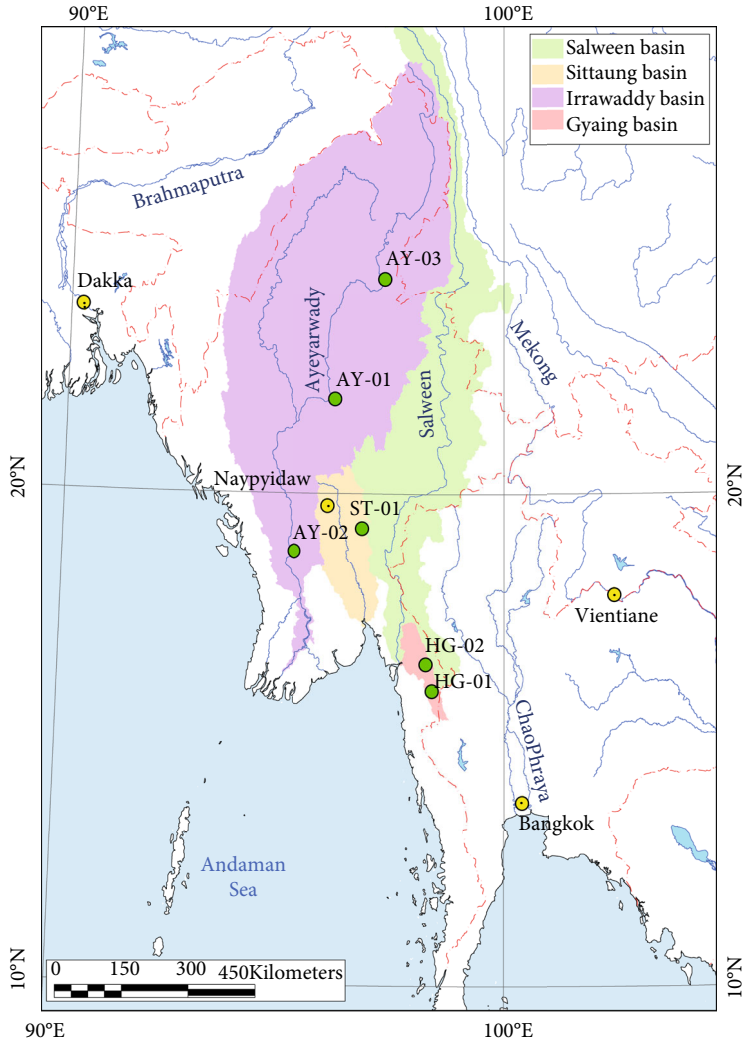

Figure 1: Map of collecting localities of Leonardo Fea in the former British Burma (Myanmar). Locality data is presented in Table 1. The map was created using ESRI ArcGIS 10 software (http://www.esri.com/arcgis). The topographic base of the map was compiled with Natural Earth Free Vector and Raster Map Data (http://www.naturalearthdata.com), GSHHG version 2.3.7 (http://www.soest.hawaii.edu/pwessel/gshhg) [71], and the HydroSHEDS database (http://www.hydrosheds.org) [72, 73]. (Map: Mikhail Yu. Gofarov).

as well as the sculpture and periostracum [17, 20]. We analyzed 88 contours of the Lamellidentini representatives, i.e. *Lamellidens generosus*, *L. savadiensis*, and *Trapezidens dolichorhynchus*, using Fourier coefficients through SHAPE v1.3 [34] as described in our previous work [19]. Contours of available Tappane-Canefri's specimens such as *Unio corrianus, U. marginalis, U. pulcher, U. protensus* var. *obtusatus, U. marginalis* var. *tricolor*, and *U. marginalis* var. *subflabellata* were also included in the analysis. Images of the shells were processed using GIMP v2.10 (http://www.gimp.org). The results of the Principal Component Analysis (PCA) of Fourier coefficients were visualized using PAST v4.06 [35]. Differences in the shell proportions of the genera *Lamellidens* and *Trapezidens* were studied using the shell elongation index (SEI = height/length ratio ×100) [36].

2.3. Molecular Analyses. New partial sequences of the mitochondrial *cytochrome c oxidase subunit I* (*COI*) and *16S ribosomal RNA* (*16S rRNA*), and the nuclear *28S ribosomal RNA* (*28S rRNA*) genes were obtained for the majority of specimens collected by us from the historical localities in Myanmar listed by Tapparone-Canefri [15] (Tables 1–3 and Table S1). PCR amplification and sequencing were carried out as described in our previous papers [17, 24, 37]. Additionally, we used available GenBank sequences from Southeast Asia published in a series of earlier works [17, 19, 20, 23, 24, 31, 37–40] (Table S1).

Molecular diagnoses for the new species described here was designed based on available sequences for *Trapezoideus* taxa [17, 20, 22] using a Toggle Conserved Sites tool of MEGA7 at 50% level [41] as decribed in our previous works [17, 24]. The uncorrected *COI p*-distances between *Trapezoideus* species were also calculated through MEGA7 [41].

2.4. Phylogenetic Analyses. We reconstructed a multi-locus phylogeny (3 codons of *COI*+*16S rRNA*+*28S rRNA*) using 120 haplotypes of the Unionidae from Myanmar (Table S1 and Alignment S1). Two representatives of the

Table 1: List of collecting localities of freshwater mussel taxa listed by C.M. Tapparone-Canefri [15] and those presented in the MSNG collection (samples of Leonardo Fea).

Code	Original label(s)	Locality data	Approximate geographic coordinates		References
			Latitude	Longitude	
HG-01	Tenasserim: Meetan, fiume Houngdarau	Mitan stream (Mitan Chaung in Burmese), a tributary of the upstream section of the Haungthayaw River, Myanmar	15.9999	98.3946	Tapparone-Canefri [15]
HG-02	Kokareet, Tenasserim	A stream at Kawkareik town, Haungthayaw Basin, Myanmar	16.5528	98.2378	Tapparone-Canefri [15]
AY-01	Mandalay; mercato di Mandalay	Ayeyarwady River and(or) floodplain lakes at Mandalay city (bought in a city market), Myanmar	21.9491	96.0483	Tapparone-Canefri [15]
AY-02	Prome, Bassa Birmania	Ayeyarwady River at Pyay city, Myanmar	18.8142	95.2138	Tapparone-Canefri [15]
AY-03	Teinzo del mule Chaung; Teinzò, N. E. di Bhamò; Teinzo, nel fiume mule, Monti E. di Bhamo; A(lta). Birmania: Teinzo	Mole stream (mole Chaung in Burmese) at Teinthaw village, Ayeyarwady Basin, Myanmar	24.3978	97.2519	Tapparone-Canefri [15]; Bolotov et al. [27]
ST-01	Carin independ. 1000-1200 m	Upstream section of the Tauk Ue Kupt River, Sittaung Basin, Myanmar	19.3075	96.7219	Bolotov et al. [28]

Margaritiferidae, i.e. *Gibbosula laosensis* (Lea, 1863) and *Margaritifera dahurica* (Middendorff, 1850), were used as outgroup. Sequences of *Trapezoideus foliaceus* (Gould, 1843) from the Mae Klong River (Thailand) were added to the dataset to provide more robust phylogenetic signal for the *Trapezoideus* clade. The maximum likelihood (ML) analysis was performed through IQ-TREE (W-IQ-TREE) server [42] using an automatic identification of the best evolutionary models [43] and an ultrafast bootstrap (UFBoot) algorithm with 5,000 replicates [44]. Models of sequence evolution for each partition were calculated through Model Finder [45] based on Bayesian Information Criterion (BIC) and were as follows: 1st codon *COI* – F81; 2nd codon *COI* – GTR + G; 3rd codon *COI* – TN + G + I; 16S – TIM2 + G + I; 28S – TIM3 + G + I. Bayesian inference analysis (BI) was carried out in MrBayes v3.2.7 [46] with two runs, each with three heated (temperature = 0.1) and one cold Markov chain, during 50×10^6 generations and sampling every 1,000th generation. The first 15% of trees were discarded as burn-in. The calculation was performed at San Diego Supercomputer Center through the CIPRES Science Gateway [47]. A trace analysis tool (Tracer v. 1.7) was used to check a convergence of the MCMC chains to a stationary distribution [48]. The effective sample size (ESS) for all the parameters was recorded as >5,000.

The mitochondrial *COI* trees were reconstructed separately for the Lamellidentini, Leoparreysiini, Indochinellini, and Contradentini tribes (Figures S2–S5, Table S1, Alignments S2–S5). Each *COI* dataset was analyzed using maximum likelihood (ML) and Bayesian inference (BI) methods mainly as stated above, but for BI analysis two independent runs of 25×10^6 generations were sampled at intervals of every 1,000th generation. The best-fit nucleotide substitution models and the partition scheme are listed in Table S2.

2.5. Nomenclatural Acts. The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (ICZN), and hence the new name and the taxonomic opinions contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank (http://zoobank.org), the online registration system for the ICZN. The LSID for this publication is: http://zoobank.org/urn:lsid:zoobank.org:pub:49FCF27F-8C9B-4235-9701-C0FDB623FD0D. The electronic edition of this paper was published in a journal with an ISSN, and has been archived and is available from PubMed Central.

3. Results

3.1. Morphological Traits and Shell Proportions of Tapparone-Canefri's Taxa. Among specimens from the MSNG collection and the taxa descriptions from Tapparone-Canefri's work [15], we identified *Indochinella pugio pugio*, *I. pugio paradoxa*, *Indonaia andersoniana*, *Radiatula chaudhurii* and *R. mouhoti haungthayawensis* (Figure 2), *Leoparreysia tavoyensis* (Figure 3), *Lamellidens generosus* (Figure 4), *L. savadiensis* and *Trapezidens dolichorhynchus* (Figure 5), *Yaukthwa nesemanni* and *Y. zayleymanensis*, as well as *Pseudodon kayinensis* (Figure 6) (see Taxonomic account below).

In the MSNG collection, the type series of only four nominal taxa described by Tapparone-Canefri [15] as new to science are still available, i.e. *Unio rectangularis* (Figure 6(d)), *U. pulcher* (Figure 4(a)), *U. protensus* var. *obtusatus* (Figure 4(e)), and *U. marginalis* var. *subflabellata* (Figure 5(e)). Accurate comparative conchological analyses of these shells supported the opinion [22] that *Unio rectangularis* is more likely representative of the Contradentini, specifically the genus *Yaukthwa*, mainly based on the rectangular shell shape and wrinkles on the posterior slope.

Table 2: Taxonomic review of freshwater mussel taxa listed by C.M. Tapparone-Canefri [15] and those presented in the MSNG collection (samples of Leonardo Fea).

Page	Nominal taxon by Tapparone-Canefri (1889 and collection labels) (original spelling and authorship)	Re-identification by Prashad (1922) (original spelling and authorship)	Label data [old locality code: See Table 1 for detail]	Modern taxonomic placement	Tapparone-Canefri's sample depository	Comments and references
355	*Pseudodon inoscularis* Gould	*Pseudodon vondembuschiana* var. *inoscularis* (Gould)	Meetan, fiume Houngdarau (L. Fea) [HG-01]	*Pseudodon kayinensis* Bolotov et al., 2020	Whereabouts unknown (probably in ZSI)	Only specimens of *Pseudodon kayinensis* were collected from the Haungthayaw Basin. Tapparone-Canefri referred to a shell image from Hanley and Theobald ([70]: Pl. IX, image 2), which is morphologically very similar to this species (this study) (Figures 6(o) and 6(p))
343	*Unio bonneaudii* Eydoux et Souleyet, 1838	*Indonaia bonneaudi* (Eydoux)	Meetan, fiume Houngdarau (L. Fea) [HG-01]	*Radiatula mouhoti haungthayawensis* Bolotov et al., 2019	Whereabouts unknown	Based on the description, distribution, and molecular data on the type series of *Radiatula mouhoti haungthayawensis* (see [23]) (Figure 2(q))
343, 344	*Unio burmanus* Blanford, 1869	N/A	Label: Teinzo del mule Chaung – Marz. 1886. L. Fea. Published label data: Teinzò, nel fiume mule, N. E. di Bhamò [AY-03]	*Radiatula chaudhurii* (Preston, 1912)	MSNG	Tapparone-Canefri's sample examined; new samples from the locality sequenced (this study) (Figures 2(n)–2(p))
344	*Unio coeruleus* Lea, 1852	*Indonaia caerulea* (Lea)	Mandalay (L. Fea) [AY-01]	*Indonaia andersoniana* (Nevill, 1877)	MSNG	Tapparone-Canefri's sample examined; new samples from the locality sequenced (this study) (Figures 2(d)-2(f), and 2(h))
347	*Unio corrianus* Lea	*Lamellidens corrianus* (Lea)	Mandalay, del mercato [AY-01]	*Lamellidens generosus* Gould, 1847)	MSNG	Based on Tapparone-Canefri's sample, description, shell shape, distribution, and DNA sequence data on new samples from Ayeyarwady Basin (this study) (Figures 4(g) and 4(h))
343	*Unio crispatus* Gould	*Indonaia crispata* (Gould)	Meetan, fiume Houngdarau (L. Fea) [HG-01]	*Indochinella pugio paradoxa* Bolotov et al., 2019	Whereabouts unknown	Based on the description, distribution, and DNA sequence data on the type series of *Indochinella pugio paradoxa* (see [23]) (Figure 2(c))
348	*Unio dolichorhynchus* Tapparone-Canefri, 1889	*Lamellidens corrianus* (Lea)	Mercato di Mandalay (L. Fea) [AY-01]	*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889)	Whereabouts unknown	Based on Prashad's ([16]: Pl. II, image 11) image of *Unio dolichorhynchus*, the description, distribution, and DNA sequence data on topotypes ([24, 30]; this study) (Figure 5(l))
345	*Unio exsolescens* [sic.] Gould	*Trapezoideus exolescens* (Gould)	Meetan, fiume Houngdarau (L. Fea) [HG-01]	*Trapezoideus mitanensis* sp. nov.	Whereabouts unknown	Based on the description, distribution, and DNA sequence on the type series of the new species (this study) (Figures 6(l)–6(n))

Table 2: Continued.

Page	Nominal taxon by Tapparone-Canefri (1889 and collection labels) (original spelling and authorship)	Re-identification by Prashad (1922) (original spelling and authorship)	Label data [old locality code: See Table 1 for detail]	Modern taxonomic placement	Tapparone-Canefri's sample depository	Comments and references
340	*Unio feae* Tapparone-Canefri, 1889	*Parreyssia feae* (Tapparone-Canefri)	Meetan, fiume Houngdarau (L. Fea in numerosi esemplari) [HG-01]	*Leoparreysia tavoyensis* (Gould, 1843)	MNHN; ZSI	Tapparone-Canefri's sample examined; new topotypes from the Haungthayaw River sequenced (this study) (Figures 3(h) and 3(i)).
345	*Unio foliaceus* Gould	*Trapezoideus foliaceus* (Gould)	Label: "A(lta). Birmania: Teinzo". Published data: Teinzò, N. E. di Bhamò (L. Fea) [AY-03]	*Yaukthwa zayleymanensis* (Preston, 1912)	MSNG	Tapparone-Canefri's sample examined; new topotypes from the locality sequenced (this study) (Figures 6(h)–6(k))
352	*Unio generosus* Gould	*Lamellidens generosus* (Gould)	Bhamò; Meetan, fiume Houngdarau (L. Fea, esemplari tipici) [HG-01]; Mercato di Mandalay (L. Fea) [AY-01]	*Lamellidens generosus* (Gould, 1847)	Whereabouts unknown	Based on the description, distribution, and DNA sequence data on new samples from the Haungthayaw River (this study)
352	*Unio generosus* var. *delapsus* Tapparone-Canefri, 1889	*Lamellidens generosus* (Gould)	Meetan, fiume Houngdarau (L. Fea) [HG-01]; Mercato di Mandalay (L. Fea) [AY-01]	*Lamellidens generosus* (Gould, 1847)	Whereabouts unknown	Based on the description, distribution, shell proportions, and new samples from the Haungthayaw River (this study)
353	*Unio gianellii* Tapparone-Canefri, 1889	*Lamellidens scutum* (Sowerby)	Mercato di Mandalay (L. Fea) [AY-01]	*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889)	Whereabouts unknown	Based on the description, shell proportions, distribution and new samples from Mandalay (this study) (Figure 5(j))
354	*Unio gianelli* var. *degener* Tapparone-Canefri, 1889	*Lamellidens scutum* (Sowerby)	Mercato di Mandalay (L. Fea) [AY-01]	*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889)	Whereabouts unknown	Based on the description, shell proportions, distribution, and new samples from Mandalay (this study)
341	*Unio houngdarauicus* Tapparone-Canefri, 1889 syn. Nov.	*Parreyssia houngdaranicus* (sic.) (Tapparone-Canefri)	Meetan, fiume Houngdarau (L. Fea) [HG-01]	*Leoparreysia tavoyensis* (Gould, 1843)	MNHN	Tapparone-Canefri's sample examined; new samples from Haungthayaw River sequenced (this study) (Figure 3(j))
344	*Unio leioma* Benson, 1862	*Indonaia caerulea* (Lea)	Mercato di Mandalay (L. Fea, con moltissimi *U. crispatus*) [AY-01]	*Indonaia andersoniana* (Nevill, 1877)	Whereabouts unknown	Based on the description, distribution, and DNA sequence data on new samples from Mandalay (Figures 2(l) and 2(m))
342	*Unio mandelayensis* Theobald, 1873	*Parreyssia mandelayensis* (Theobald)	Mercato di Mandalay (L. Fea) [AY-01]	*Leoparreysia tavoyensis* (Gould, 1843)	Whereabouts unknown	Based on the description, distribution, and DNA sequence data on new samples from Mandalay (Figure 3(g))
345	*Unio marginalis* Lamarck	*Lamellidens marginalis* (Lamarck)	Mercato di Mandalay (L. Fea) [AY-01]	*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889)	Whereabouts unknown	Based on Tapparone-Canefri's sample morphology, the description, distribution, and shell proportions (Figure 5(m))
347	*Unio marginalis* var. *bilineata* Hanley & Theobald	Not listed	Mandalay (L. Fea) [AY-01]	*Indonaia andersoniana* (Nevill, 1877)	MSNG	Tapparone-Canefri's sample examined; new samples from the locality sequenced (this study) (Figures 2(g) and 2(i))

Table 2: Continued.

Page	Nominal taxon by Tapparone-Canefri (1889 and collection labels) (original spelling and authorship)	Re-identification by Prashad (1922) (original spelling and authorship)	Label data [old locality code: See Table 1 for detail]	Modern taxonomic placement	Tapparone-Canefri's sample depository	Comments and references
346	*Unio marginalis* var. *cylindrica* Hanley & Theobald	*Lamellidens marginalis* (Lamarck)	Mercato di Mandalay (L. Fea) [AY-01]	*Lamellidens savadiensis* (Nevill, 1877)	Whereabouts unknown	Based on the image of the specimen ([55]: Pl. XLIV, image 1), description and new sequenced samples from the locality (this study)
346	*Unio marginalis* var. *obesa* Hanley & Theobald	*Lamellidens marginalis* (Lamarck)	Mercato di Mandalay (L. Fea) [AY-01]	*Lamellidens generosus* (Gould, 1847)	Whereabouts unknown	Based on the description, distribution, and DNA sequence data on new samples from Ayeyarwady Basin (this study)
346	*Unio marginalis* var. *subflabellata* Tapparone-Canefri, 1889	*Lamellidens marginalis* (Lamarck)	Mandalay, del mercato (L. Fea) [AY-01]	*Lamellidens savadiensis* (Nevill, 1877)	MSNG	Tapparone-Canefri's sample examined (this study); new samples from the locality sequenced (this study) (Figures 5(e), 5(g), and 5(h))
347	*Unio marginalis* var. *tricolor* Hanley & Theobald	*Lamellidens generosus* (Gould)	Mandalay, del mercato (L. Fea) [AY-01]	*Lamellidens savadiensis* (Nevill, 1877)	MSNG	Tapparone-Canefri's sample examined (this study); new samples from the locality sequenced (this study) (Figures 5(d) and 5(f))
346	*Unio marginalis* var. *zonata* Hanley & Theobald	*Lamellidens generosus* (Gould)	Kokareet, Tenasserim (L. Fea) [HG-02]	*Lamellidens generosus* (Gould, 1847)	Whereabouts unknown	Based on the description, distribution, and DNA sequence data on new samples from the locality (Figure 4(d))
339	*Unio Parma*, Benson, ex reeve	*Parreyssia tavoyensis* (Gould)	Meetan, fiume Houngdarau (L. Fea) [HG-01]	*Leoparreysia tavoyensis* (Gould, 1843)	Whereabouts unknown	Based on the description, distribution, and DNA sequence data on topotypes of *Unio Parma* from the Tanintharyi River and a sample from the Haungthayaw River (Figure 3(d))
349	*Unio protensus* Tapparone-Canefri, 1889	*Lamellidens corrianus* (Lea)	Prome, Bassa Birmania (L. Fea) [AY-02]	*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889)	Whereabouts unknown	Based on Prashad's ([16]: Pl. II, image 9) image of *Unio protensus*, the description, distribution and new sequenced samples (this study) (Figure 5(i))
350	*Unio protensus* var. *ellipticus* Tapparone-Canefri, 1889	*Lamellidens corrianus* (Lea)	Prome, Bassa Birmania (L. Fea) [AY-02]	*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889)	Whereabouts unknown	Based on Prashad's image of *Unio protensus* var. *ellipticus* ([16]: Pl. II, image 10), description, shell proportions, distribution and new sequenced samples (this study) (Figure 5(k))
350	*Unio protensus* var. *obtusatus* Tapparone-Canefri, 1889	*Lamellidens marginalis* (Lamarck)	Prome, Bassa Birmania (L. Fea) [AY-02]	*Lamellidens generosus* (Gould, 1847)	MSNG	Based on examined holotype, description, shell proportions, distribution, and new sequenced samples (this study) (Figures 4(e) and 4(f))

Table 2: Continued.

Page	Nominal taxon by Tapparone-Canefri (1889 and collection labels) (original spelling and authorship)	Re-identification by Prashad (1922) (original spelling and authorship)	Label data [old locality code: See Table 1 for detail]	Modern taxonomic placement	Tapparone-Canefri's sample depository	Comments and references
344	*Unio pugio* Benson, 1862	*Oxynaia pugio* (Benson)	Label: "Mandalay, del mercato" [AY-01]. Published label data: Prome, Bassa Birmania (L. Fea, pochi esemplari) [AY-02]; mercato di Mandalay (L. Fea, esemplari numerosissimi) [AY-01]	*Indochinella pugio pugio* (Benson, 1862)	MSNG	Tapparone-Canefri's sample examined; new sample from Mandalay sequenced (this study) (Figures 2(a) and 2(b))
350	*Unio pulcher* Tapparone-Canefri, 1889	*Lamellidens generosus* (Gould)	Tenasserim: Meetan, del fiume Houngdarau. Leg. L. Fea [HG-01]	*Lamellidens generosus* (Gould, 1847)	MSNG	Based on the syntypes, description, shell proportions, distribution, and new samples from the type locality (this study) (Figures 4(a) and 4(b))
351	*Unio pulcher* var. *lamellatiformis* Tapparone-Canefri, 1889	*Lamellidens generosus* (Gould)	Meetan, fiume Houngdarau (L. Fea) [HG-01]	*Lamellidens generosus* (Gould, 1847)	Whereabouts unknown	Based on the description, shell proportions, distribution and new samples from the type locality
351	*Unio pulcher* var. *ponderosulus* Tapparone-Canefri, 1889	*Lamellidens lamellatus* (Lea)	Meetan, fiume Houngdarau (L. Fea) [HG-01]	*Lamellidens generosus* (Gould, 1847)	Whereabouts unknown	Based on the description, shell proportions, distribution, and new samples from the type locality
354	*Unio rectangularis* Tapparone-Canefri, 1889	*Margaritanopsis laosensis* (Lea)	Teinzo, nel fiume mule, Monti E. di Bhamo (L. Fea) [AY-03]	*Yaukthwa rectangularis* (Tapparone-Canefri, 1889)	MSNG	Holotype examined [27]; new topotypes sequenced (this study) (Figures 5(d) and 5(e))
N/A	*Unio Sella* Tapparone-Canefri, unpublished name	*Margaritanopsis laosensis* (Lea)	Carin independ. 1000-1200 m [ST-01]	*Yaukthwa nesemanni* (Konopleva, Bolotov & Kondakov, 2017) (=*Unio sella* Prashad, 1922; unavailable name, introduced as a synonym)	MSNG	Earlier, the lectotype of *Unio sella* Prashad, 1922 was designated and examined; topotypes sequenced [24, 28] (Figures 6(a)–6(c))
343	*Unio smaragdites* Benson, 1862 (this shell is labelled as "*Unio scobinatus* Bens.??" in MSNG)	*Parreyssia smaragdites* (Benson)	Label: Mandalay, del mercato [AY-01]. Published label data: Mercato di Mandalay (L. Fea) [AY-01]	*Indonaia andersoniana* (Nevill, 1877)	MSNG	Tapparone-Canefri's sample examined; new sample from Mandalay sequenced (this study) (Figures 2(j) and 2(k))

N/A – not available.

Table 3: List of sequenced representatives of freshwater mussel taxa listed by C.M. Tapparone-Canefri [15] and several related species.

Nominal species	Modern taxonomic placement	Locality of new sample [old locality code: See Table 1 for detail] (status of sample)	Specimen voucher	GenBank acc. Numbers		
				COI	*16S rRNA*	*28S rRNA*
New taxa described by Tapparone-Canefri [15]						
Unio dolichorhynchus Tapparone-Canefri, 1889	*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889)	Mandalay [AY-01] (topotype)	RMBH biv 442/2	OL597741	n/a	n/a
Unio feae Tapparone-Canefri, 1889 syn. nov.	*Leoparreysia tavoyensis* (Gould, 1843)	Haungthayaw [close to HG-02] (topotype)	RMBH biv 362/3	MK372425	n/a	n/a
Unio generosus var. *delapsus* Tapparone-Canefri, 1889 syn. nov.	*Lamellidens generosus* (Gould, 1847)	Mitan stream, Haungthayaw Basin [HG-01] (topotype)	RMBH biv 1024/3	OL597808	n/a	n/a
Unio gianellii Tapparone-Canefri, 1889 syn. nov.	*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889)	Mandalay [AY-01] (topotype)	RMBH biv 423	n/a	n/a	n/a
Unio gianelli var. *degener* Tapparone-Canefri, 1889 syn. nov.	*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889)	Mandalay [AY-01] (topotype)	RMBH biv 417/8	n/a	n/a	n/a
Unio houngdarauicus Tapparone-Canefri, 1889 syn. nov.	*Leoparreysia tavoyensis* (Gould, 1843)	Haungthayaw [close to HG-02] (topotype)	RMBH biv 362/2	MK372424	n/a	n/a
Unio marginalis var. *subflabellata* Tapparone-Canefri, 1889 syn. nov.	*Lamellidens savadiensis* (Nevill, 1877)	Mandalay [AY-01] (topotypes)	RMBH biv 427A/1	OL597754	n/a	n/a
			RMBH biv 427A/2	OL597755	n/a	n/a
Unio protensus Tapparone-Canefri, 1889 syn. nov.	*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889)	Mandalay [350 km N of AY-02] (non-topotype sample)	RMBH biv 442/1	OL597740	n/a	n/a
Unio protensus var. *ellipticus* Tapparone-Canefri, 1889 syn. nov.	*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889)	Nyang-U [260 km N of AY-02] (non-topotype sample)	RMBH biv 417/2	MN780886	n/a	n/a
Unio protensus var. *obtusatus* Tapparone-Canefri, 1889 syn. nov.	*Lamellidens generosus* (Gould, 1847)	Pyay [AY-02] (topotypes)	RMBH biv 672/1	OL597804	n/a	n/a
			RMBH biv 672/2	OL597805	n/a	n/a
Unio pulcher Tapparone-Canefri, 1889 syn. nov.	*Lamellidens generosus* (Gould, 1847)	Mitan stream, Haungthayaw Basin [HG-01] (topotype)	RMBH biv 1024/1	OL597806	OL598379	n/a
Unio pulcher var. *lamellatiformis* Tapparone-Canefri, 1889 syn. nov.	*Lamellidens generosus* (Gould, 1847)	Mitan stream, Haungthayaw Basin [HG-01] (topotype)	RMBH biv 1024/5	n/a	n/a	n/a
Unio pulcher var. *ponderosulus* Tapparone-Canefri, 1889	*Lamellidens generosus* (Gould, 1847)	Haungthayaw [close to HG-01] (topotype)	RMBH biv 1024/2	OL597807	n/a	n/a

Table 3: Continued.

Nominal species	Modern taxonomic placement	Locality of new sample [old locality code: See Table 1 for detail] (status of sample)	Specimen voucher	GenBank acc. Numbers		
				COI	*16S rRNA*	*28S rRNA*
			RMBH biv 916/1	OL597635	ON142664	OL598387
Unio rectangularis Tapparone-Canefri, 1889	*Yaukthwa rectangularis* (Tapparone-Canefri, 1889)	Mole stream at Teinthaw village [AY-03] (topotypes)	RMBH biv 916/2	OL597636	ON142665	OL598388
			RMBH biv 916/3	OL597637	n/a	n/a
			RMBH biv 917/1	OL597638	ON142666	OL598389
Taxonomic opinions of Tapparone-Canefri [15]						
Pseudodon inoscularis Tapparone-Canefri, 1889	*Pseudodon kayinensis* Bolotov et al., 2020	Mitan stream, Haungthayaw Basin [HG-01] (new sample)	RMBH biv 1026/1	OL597610	n/a	n/a
			RMBH biv 1026/2	OL597611	n/a	n/a
			RMBH biv 1026/3	OL597612	n/a	n/a
Unio bonneaudii Tapparone-Canefri, 1889	*Radiatula mouhoti haungthayawensis* Bolotov et al., 2019	Haungthayaw [sample RMBH biv360 close to HG-02 and RMBH biv1023 corresponds to HG-01] (new samples)	RMBH biv 360/1	MK372417	MK372463	MK372493
			RMBH biv 360/2	MK372418	MK372464	MK372494
			RMBH biv 360/3	MK372419	n/a	MK372495
			RMBH biv 1023/1	OL597713	n/a	n/a
			RMBH biv 1023/2	OL597714	OL598374	n/a
			RMBH biv 1023/3	OL597715	n/a	n/a
Unio burmanus Tapparone-Canefri, 1889	*Radiatula chaudhurii* (Preston, 1912)	Ayeyarwady River at Bhamo city [close to AY-03] (new sample)	RMBH biv 260/5	MF352266	MF352330	MF352390
			RMBH biv 260/9	MF352267	MF352331	MF352391
			RMBH biv 260/10	MF352268	MF352332	MF352392
Unio coeruleus Tapparone-Canefri, 1889	*Indonaia andersoniana* (Nevill, 1877)	Mandalay [AY-01] (new sample)	RMBH biv 429/1	OL597692	n/a	n/a
Unio crispatus Tapparone-Canefri, 1889	*Indochinella pugio paradoxa* Bolotov et al., 2019	Haungthayaw [close to HG-02] (new sample)	RMBH biv 361/1	MK372420	MK372465	MK372496
			RMBH biv 361/2	MK372421	MK372466	MK372497
			RMBH biv 361/3	MK372422	MK372467	MK372498
Unio corrianus Tapparone-Canefri, 1889	*Lamellidens generosus* (Gould, 1847)	Mandalay [AY-01] (new sample)	RMBH biv 356/1	OL597760	n/a	n/a
			RMBH biv 356/2	OL597761	n/a	OL598400
			RMBH biv 356/3	OL597762	n/a	n/a

Table 3: Continued.

Nominal species	Modern taxonomic placement	Locality of new sample [old locality code: See Table 1 for detail] (status of sample)	Specimen voucher	GenBank acc. Numbers		
				COI	*16S rRNA*	*28S rRNA*
Unio exsolescens Tapparone-Canefri, 1889	*Trapezoideus mitanensis* sp. nov.	Mitan stream, Haungthayaw Basin [HG-01] (new sample)	RMBH biv 1021/1	OL597613	ON142670	ON171238
			RMBH biv 1021/2	OL597614	OL598370	OL598384
			RMBH biv 1021/3	OL597615	n/a	n/a
Unio foliaceus Tapparone-Canefri, 1889	*Yaukthwa zayleymanensis* (Preston, 1912)	Tarkat stream, Ayeyarwady Basin [100 km N of AY-03] (new sample)	RMBH biv 679/1	MN275074	MN307261	MN307203
			RMBH biv 679/2	MN275075	MN307262	MN307204
			RMBH biv 679/3	OL597658	n/a	
Unio generosus Tapparone-Canefri, 1889	*Lamellidens generosus* (Gould, 1847)	Mitan stream, Haungthayaw Basin [HG-01] (new sample)	RMBH biv 1024/4	n/a	n/a	n/a
Unio leioma Tapparone-Canefri, 1889	*Indonaia andersoniana* (Nevill, 1877)	Mandalay [AY-01] (new sample)	RMBH biv 434	OL597695	n/a	n/a
Unio marginalis Tapparone-Canefri, 1889	*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889)	Mandalay [AY-01] (new sample)	RMBH biv 417/3	MN780887	n/a	n/a
Unio marginalis var. *bilineata* Tapparone-Canefri, 1889	*Indonaia andersoniana* (Nevill, 1877)	Mandalay [AY-01] (new sample)	RMBH biv 429/2	OL597693	n/a	n/a
Unio marginalis var. *cylindrica* Tapparone-Canefri, 1889	*Lamellidens savadiensis* (Nevill, 1877)	Mandalay [AY-01] (new sample)	RMBH biv 416/3	OL597753	n/a	n/a
Unio marginalis var. *obesa* Tapparone-Canefri, 1889	*Lamellidens generosus* (Gould, 1847)	Mandalay [AY-01] (new sample)	RMBH biv 356/10	n/a	n/a	n/a
Unio marginalis var. *tricolor* Tapparone-Canefri, 1889	*Lamellidens savadiensis* (Nevill, 1877)	Mandalay [AY-01] (new sample)	RMBH biv 442/3	OL597756	n/a	n/a
Unio marginalis var. *zonata* Tapparone-Canefri, 1889	*Lamellidens generosus* (Gould, 1847)	Haungthayaw [close to HG-02] (new sample)	RMBH biv 363/1	OL597768	n/a	OL598403
			RMBH biv 363/2	OL597769	n/a	n/a
			RMBH biv 363/3	OL597770	n/a	n/a
			RMBH biv 364/1	OL597771	n/a	OL598404
			RMBH biv 364/3	OL597772	n/a	n/a
Unio parma Tapparone-Canefri, 1889	*Leoparreysia tavoyensis* (Gould, 1843)	Haungthayaw [close to HG-02] (new sample)	RMBH biv 362/1	MK372423	n/a	MK372499
Unio pugio Tapparone-Canefri, 1889	*Indochinella pugio pugio* (Benson, 1862)	Mandalay [AY-01] (new sample)	RMBH biv 441/2	n/a	n/a	n/a

Table 3: Continued.

Nominal species	Modern taxonomic placement	Locality of new sample [old locality code: See Table 1 for detail] (status of sample)	Specimen voucher	GenBank acc. Numbers		
				COI	*16S rRNA*	*28S rRNA*
Unio smaragdites Tapparone-Canefri, 1889	*Indonaia andersoniana* (Nevill, 1877)	Mandalay [AY-01] (new sample)	RMBH biv 450/1	OL597696	n/a	n/a
			RMBH biv 450/2	OL597697	n/a	n/a
Related nominal taxa						
Unio bhamoensis Theobald, 1873	*Leoparreysia tavoyensis* (Gould, 1843)	Bhamo (topotypes)	RMBH biv 266/4	MF352280	MF352343	MF352400
			RMBH biv 266/5	MF352281	MF352344	MF352401
			RMBH biv 266/6	MF352282	MF352345	MF352402
Unio generosus Gould, 1847	*Lamellidens generosus* (Gould, 1847)	Hlaingbwe River (topotypes)	RMBH biv 636/1	OL597799	n/a	n/a
			RMBH biv 636/2	OL597800	OL598377	OL598409
			RMBH biv 636/3	OL597801	OL598378	OL598410
Unio mandelayensis Theobald, 1873	*Leoparreysia tavoyensis* (Gould, 1843)	Mandalay (topotypes from AY-01)	RMBH biv 447/1	OL597863	n/a	n/a
			RMBH biv 447/2	OL597864	n/a	n/a
Unio parma Sowerby, 1868	*Leoparreysia tavoyensis* (Gould, 1843)	Tanintharyi (Tenasserim) river (topotypes)	RMBH biv 634/1	OL597865	OL598381	OL598417
			RMBH biv 634/2	OL597866	OL598382	OL598418
			RMBH biv 634/3	OL597867	OL598383	OL598419
Unio sella Prashad, 1922 (unavailable name)	*Yaukthwa nesemanni* (Konopleva, Bolotov & Kondakov, 2017)	Tauk Ue Kupt River (topotypes)	RMBH: Biv 144/14	KX865906	KX865663	KX865777
			RMBH: Biv 144/25	KX865907	KX865664	KX865778
			RMBH: Biv 144/19	KX865908	KX865665	KX865779
			RMBH: Biv 255/2	MF352254	n/a	MF352379
			RMBH: Biv 255/3	MF352255	n/a	MF352380
			RMBH: Biv 255/4	MF352256	n/a	MF352381

n/a – not available. Geographic coordinates of each locality are given in Taxonomic account, Table 1 and Table S1.

Morphological features of *Unio pulcher*, *U. protensus* var. *obtusatus*, and *U. marginalis* var. *subflabellata* allow to attribute them to the genus *Lamellidens.* The two first nominal taxa most probably belong to *Lamellidens generosus*, representing different morphological forms of this species. *Unio pulcher* has a shell shape, which is typical for *L. generosus*, with a rather high wing, broad posterior margin, and a truncated slope. *Unio protensus* var. *obtusatus* shares an elongated shell with smooth dorsal margin. However, *Unio marginalis* var. *subflabellata* has characters that are more specific to *Lamellidens savadiensis* such as an elongated, usually curved posterior margin, well-pronounced growth lines, and a shallow umbo cavity.

Other available lots of Lamellidentini from the MSNG collection such as *Unio marginalis* var. *tricolor, U. corrianus*, and *U. marginalis* according to morphological features belong to *Lamellidens savadiensis* (based on the shell shape and growth lines), *L. generosus* (shell shape and teeth

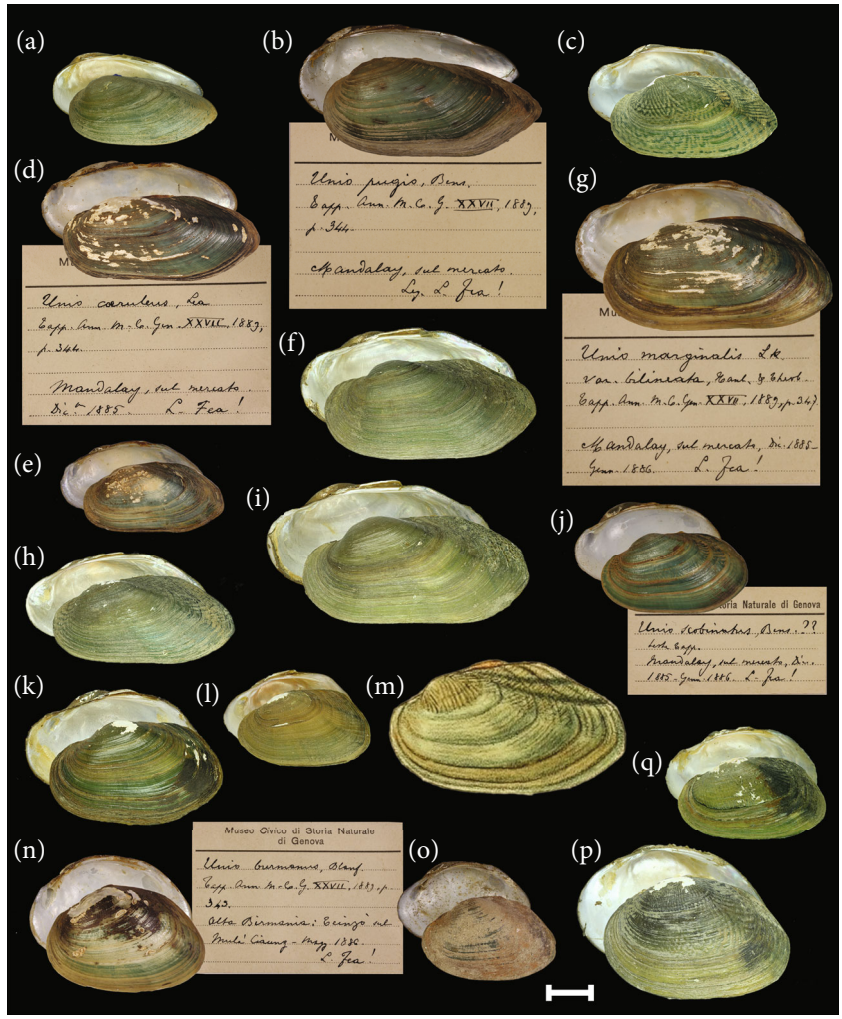

Figure 2: Shells and labels of freshwater mussel taxa sensu Tapparone-Canefri (1889) from Myanmar (Unionidae: Parreysiinae: Indochinellini). (a) *Unio pugio* (=*Indochinella pugio pugio*) (topotype RMBH biv 441/2; Sin Khong Stream, Mandalay, Ayeyarwady River basin). (b) *Unio pugio* (=*Indochinella pugio pugio*) (Tapparone-Canefri's collection; specimen MSNG with its label; Ayeyarwady River). (c) *Unio crispatus* (=*Indochinella pugio paradoxa*) (topotype RMBH biv 361/2; Haungthayaw River). (d, e) *Unio coeruleus* (=*Indonaia andersoniana*) (Tapparone-Canefri's collection; specimen MSNG with its label; Ayeyarwady River). (f) *Unio coeruleus* (=*Indonaia andersoniana*) (specimen RMBH biv 429/1; Ayeyarwady Basin). (g) *Unio marginalis* var. *bilineata* (=*Indonaia andersoniana*) (Tapparone-Canefri's collection; specimen MSNG with its label; Ayeyarwady River). (h) *Unio coeruleus* (=*Indonaia andersoniana*) (specimen RMBH biv 440; Ayeyarwady Basin). (i) *Unio marginalis* var. *bilineata* (=*Indonaia andersoniana*) (specimen RMBH biv 429/2; Ayeyarwady Basin). (j) *Unio smaragdites*, *U. scobinatus* (=*Indonaia andersoniana*) (Tapparone-Canefri's collection; specimen MSNG with its label; Ayeyarwady River). (k) *Unio smaragdites* (=*Indonaia andersoniana*) (specimen RMBH biv 450/4; Ayeyarwady Basin). (l) *Unio leioma* (=*Indonaia andersoniana*) (specimen RMBH biv 434; Ayeyarwady River). (m) *Unio leioma* (=*Indonaia andersoniana*) ([70]: pl. XII, Image 6a). (n, o) *Unio burmanus* (=*Radiatula chaudhurii*) (Tapparone-Canefri's collection; specimen MSNG; Mole Stream, Ayeyarwady Basin). (p) *Unio burmanus* (=*Radiatula chaudhurii*) (topotype RMBH biv 920/3; Mole Stream, Ayeyarwady Basin). (q) *Unio bonneaudii* (=*Radiatula mouhoti haungthayawensis*) (topotype RMBH biv 360/3; Haungthayaw River). Scale bar = 1 cm. Photos: E.S. Konopleva (a, c, f, h, i, k, l, p, q] and I.V. Vikhrev (b, d, e, g, j, n, o).

structure), and *Trapezidens dolichorhynchus* (teeth structure and pronounced muscle attachment scars), respectively. Lots listed by Tapparone-Canefri as *Unio coeruleus*, *U. marginalis* var. *bilineata*, and *U. scobinatus* have similar morphological traits such as an elongated shell with broad posterior margin, prominent umbo, thick lamella-like pseudocardinal teeth, and a deep umbo cavity, which mainly correspond to *Indonaia andersoniana*. Two specimens identified by Tapparone-Canefri as *Unio burmanus* more likely represent *Radiatula chaudhurii* having an oval-rounded shell shape with a smooth umbo, w-shaped sculpture, thick pseudocardinal teeth, and rather deep muscle attachment scars.

According to the PCA based on Fourier coefficients, four principal components (PCs) were obtained (Figure 7). A Kruskal-Wallis test revealed two significant components PC1 and PC2 ($P < 0.05$), which explained 76.9% and 12.7% of the total shell shape variance, respectively. The PC1 reflects height of the shell and shifts from an oval-elongated contour to a contour with well-developed wing and curved ventral margin. PC2 shows variation in the

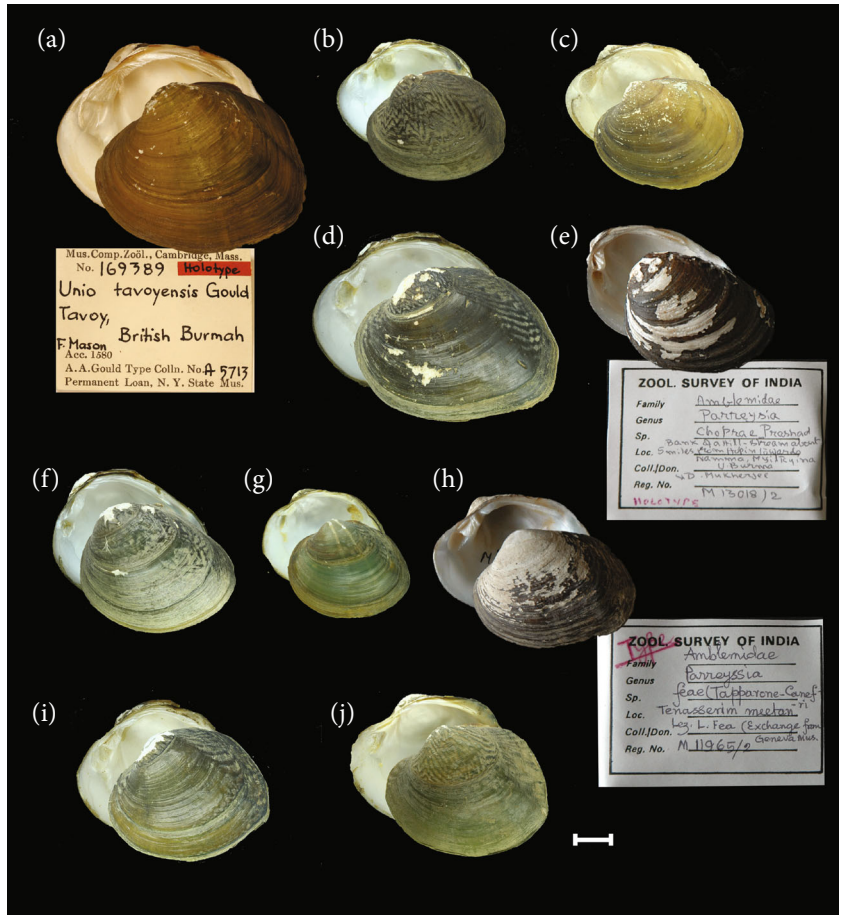

FIGURE 3: Shells of conchological varieties (ecotypes) of *Leoparreysia tavoyensis* (Gould, 1843) from Myanmar (Unionidae: Parreysiinae: Leoparreysiini). (a) *Unio tavoyensis* Gould, 1843 [1] (syntype MCZ 169389; Dawei (Tavoy) River). (b) *Unio tavoyensis* (topotype RMBH biv149; Dawei (Tavoy) River). (c) *Unio luteus* Lea, 1856 (topotype RMBH 641A; Hlaingbwe River). (d) *Unio parma* Sowerby, 1868 (topotype RMBH biv 634/2; Tenasserim River). (e) *Parreysia choprae* Prashad, 1930 (holotype ZSI M 13018/2; bank of a hill-stream about 5 miles from Hopin towards Namna, Myitkyina). (f) *Unio bhamoensis* Theobald, 1873 (topotype RMBH biv 266/6; Ayeyarwady River). (g) *Unio mandelayensis* Theobald, 1873 (topotype RMBH biv 447/1; Ayeyarwady River). (h) *Unio feae* Tapparone-Canefri, 1889 (syntype ZSI M11965/2; Mitan Stream, Haungthayaw River basin). (i) *Unio feae* Tapparone-Canefri, 1889 (topotype RMBH biv 362/3; Haungthayaw River). (j) *Unio houngdarauicus* Tapparone-Canefri, 1889 (topotype RMBH biv 362/2; Haungthayaw River). Scale bar = 1 cm. Photos: E.S. Konopleva (a–d, f, g, i, j) and N. V. Subba Rao and R. Pasupuleti (e, h).

posterior and ventral margins from a shell with almost straight ventral and truncated dorsal sides to a shell with concave ventral and dorsal margins. For *Lamellidens generosus*, *L. savadiensis*, and *Trapezidens dolichorhynchus*, we observed both distinct and transition areas of 95% confidence ellipses. Only *Unio pulcher* and *U. corrianus* fall into the distinct area of *Lamellidens generosus*, while the rest of the studied Tapparone-Canefrii's taxa belong to the transition areas. Nevertheless, *Unio marginalis* is almost completely correspond to the coordinates of a *Trapezidens dolichorhynchus* sample, whereas the dots of *U. marginalis* var. *tricolor*, *U. protensus* var. *obtusatus*, and *Unio marginalis* var. *subflabellata* mainly situated within an assemblage of *Lamellidens generosus* dots.

The mean values of the shell elongation index (SEI ± s.e.m.) for *Trapezidens* and *Lamellidens* taxa are 2.03 ± 0.03 (N = 22) and 1.76 ± 0.03 (N = 48), respectively (Mann–Whitney test: U = 115, P < 0.00001). According to the shell length vs shell width scatterplot, the trend lines of both genera are separated, but their 95% confidence ellipses are transversed (Figure S1). Such Tapparone-Canefri's nominal taxa as *Unio pulcher*, *U. pulcher* var. *ponderosulus*, and *U. pulcher* var. *lamellatiformis* fall into the 95% confidence ellipses of the genus *Lamellidens*. *U. protensus* fall into the 95% confidence ellipses of the genus *Trapezidens*. In turn, *Unio gianelli*, *U. gianelli* var. *degener*, *U. protensus* var. *ellipticus*, *U. generosus* var. *delapsus* and *U. protensus* var. *obtusatus* stand in the transition area of *Lamellidens* and *Trapezidens*.

3.2. Phylogeny of the Unionidae from Myanmar. Phylogenetic studies of freshwater mussels from Myanmar based on the multi-locus phylogeny (3 codons of *COI*+16*S rRNA*+28*S rRNA*) revealed 47 species, belonging to 12 genera, i.e. *Pseudodon, Monodontina, Sundadontina* (Pseudodontini), *Trapezoideus, Yaukthwa* (Contradentini), *Trapezidens, Lamellidens* (Lamellidentini), *Parreysia* (Parreysiini), *Leoparreysia*

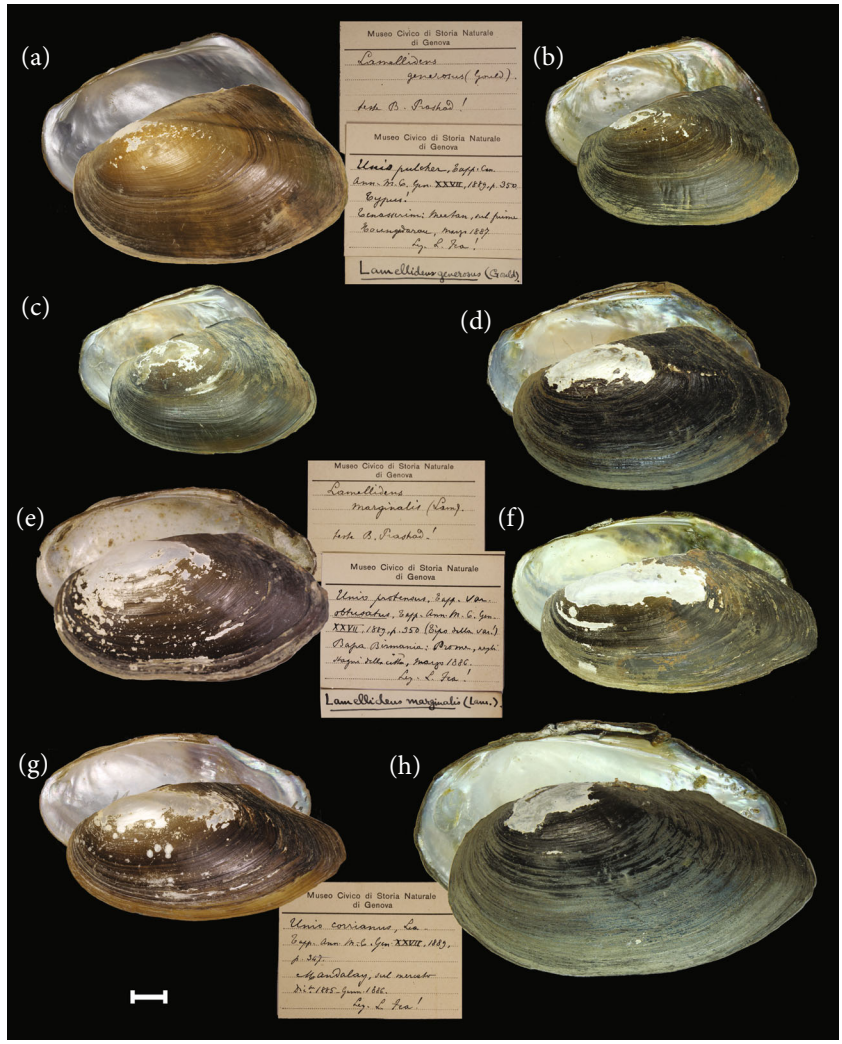

FIGURE 4: Shells of conchological varieties of *Lamellidens generosus* (Gould, 1847) from Myanmar (Unionidae: Parreysiinae: Lamellidentini). (a) *Unio pulcher* (=*Lamellidens generosus*) (Tapparone-Canefri's collection; syntype MSNG with its labels). (b) *Unio pulcher* (=*Lamellidens generosus*) (topotype RMBH biv 1024/1; Mitan Stream, Haungthayaw River basin). (c) *Unio generosus* (=*Lamellidens generosus*) (topotype RMBH biv 636/3; Hlaingbwe Basin). (d) *Unio marginalis* var. *zonata* (=*Lamellidens generosus*) (topotype RMBH biv 364/3; a stream near Kawkareik town, Haungthayaw River). (e) *Unio protensus* var. *obtusatus* (=*Lamellidens generosus*) (Tapparone-Canefri's collection; holotype MSNG with its labels). (f) *Unio protensus* var. *obtusatus* (=*Lamellidens generosus*) (topotype RMBH biv 672/2; Nga Wun River near Pyay city, Ayeyarwady Basin). (g) *Unio corrianus* (=*Lamellidens generosus*) (Tapparone-Canefri's collection; specimen MSNG with its label). (h) *Unio corrianus* (=*Lamellidens generosus*) (RMBH biv 356/2; a fish pond near Kalemyo, Ayeyarwady Basin). Scale bar = 1 cm. Photos: I.V. Vikhrev (a, e, g) and E.S. Konopleva (b-d, f, h).

(Leoparreysiini), *Indonaia, Radiatula*, and *Indochinella* (Indochinellini) (Figure 8, Figures S2–S5). Prospective topotypes of Tapparone-Canefri's *Unio coeruleus*, *U. marginalis* var. *bilineata*, and *U. scobinatus* collected from the Ayeyarwady Basin are actually repesentatives of a species-level clade corresponding to *Indonaia andersoiana* (Figure S2). Newly collected topotypes of *Unio luteus* Lea, 1856, *U. bhamoensis* Theobald, 1873, *U. mandelayensis* Theobald, 1873, *U. feae* Tapparone-Canefri, 1889, and *U. houngdarauicus* Tapparone-Canefri, 1889, morphologically distinguished from each other by the shell shape, and the sculpture and coloration of periostracum are actually representatives of a single species, *Leoparreysia tavoyensis* (Gould, 1843) (Figure 3, Figure S3).

Topotypes of *Unio protensus* var. *obtusatus* from the Nga Wun River near the city of Pyay (Ayeyarwady Basin) and *U. pulcher* from the Mitan Stream (Haungthayaw Basin) fall into the *Lamellidens generosus* clade (Figure S4). Among the specimens of *Lamellidens* from Mandalay we found only representatives of *L. savadiensis* (Figure S4). Topotypes of *Unio rectangularis* collected from the Mole Stream (Ayeyarwady Basin) phylogenetically correspond to the *Yaukthwa* clade (Figure S5).

A species that was identified by Tapparone-Canefri [15] as *Unio exolescens* from the Mitan Stream, a tributary of the Haungthayaw River, is described here as *Trapezoideus mitanensis* sp. nov. It represents a separate phylogenetic lineage that is more closely related to *Trapezoideus lenya* Bolotov

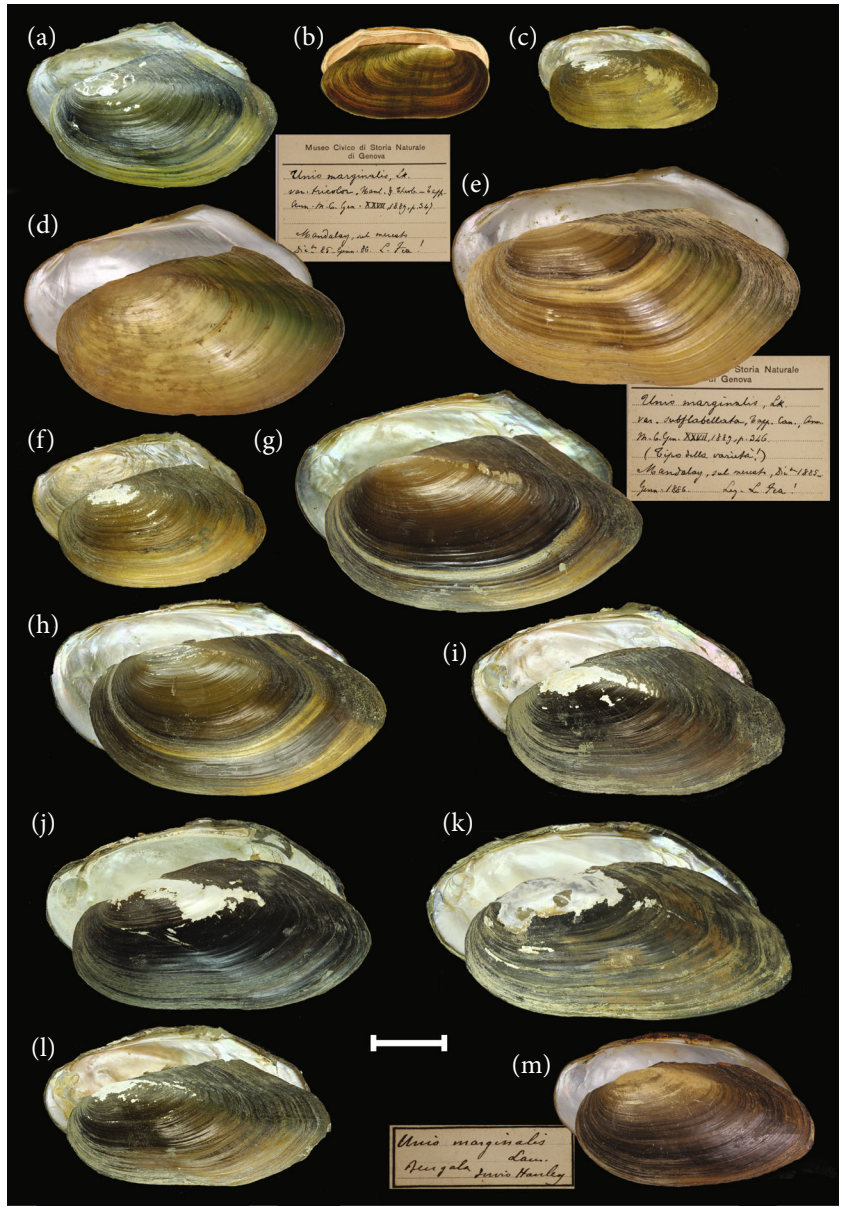

Figure 5: Shells of conchological varieties of *Lamellidens savadiensis* (Nevill, 1877) and *Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889) from Myanmar (Unionidae: Parreysiinae: Lamellidentini). (a) *Lamellidens savadiensis* (topotype RMBH biv 261/7; Shwe Kyi Lake near Bhamo, Ayeyarwady Basin). (b) *Unio marginalis* var. *cylindrica* ([55]: pl. XLIV, image 1). (c) *Unio marginalis* var. *cylindrica* (=*Lamellidens savadiensis*) (specimen RMBH biv 416/3; Mone Ding Dam outlet, Ayeyarwady Basin). (d) *Unio marginalis* var. *tricolor* sensu Tapparone-Canefri, 1889 (=*Lamellidens generosus*) (Tapparone-Canefri's collection; specimen MSNG with its label). (e) *Unio marginalis* var. *subflabellata* (=*Lamellidens savadiensis*) (Tapparone-Canefri's collection; holotype MSNG with its label). (f) *Unio marginalis* var. *tricolor* sensu Tapparone-Canefri, 1889 (=*Lamellidens generosus*) (topotype RMBH biv 442/3; Ayeyarwady River at Mandalay). (g) *Unio marginalis* var. *subflabellata* (=*Lamellidens savadiensis*) (topotype RMBH biv 427A/2; ox-bow lake, Ayeyarwady Basin at Mandalay). (h) *Unio marginalis* var. *subflabellata* (=*Lamellidens savadiensis*) (topotype RMBH biv 427A/3; ox-bow lake, Ayeyarwady Basin at Mandalay). (i) *Unio protensus* (=*Trapezidens dolichorhynchus*) (topotype RMBH biv 442/1; Ayeyarwady River at Mandalay). (j) *Unio gianellii* (=*Trapezidens dolichorhynchus*) (topotype RMBH biv 423; Ayeyarwady River at Mandalay). (k) *Unio protensus* var. *ellipticus* (=*Trapezidens dolichorhynchus*) (topotype RMBH biv 417/2; Ayeyarwady River). (l) *Unio dolichorhynchus* (=*Trapezidens dolichorhynchus*) (topotype RMBH biv RMBH biv 442/2; Ayeyarwady River at Mandalay). (m) *Unio marginalis* (=*Trapezidens dolichorhynchus*) (Tapparone-Canefri's collection; specimen MSNG with its label; Mandalay market). Scale bar = 2 cm. Photos: E.S. Konopleva (a, c, f–l) and I.V. Vikhrev (d, e, m).

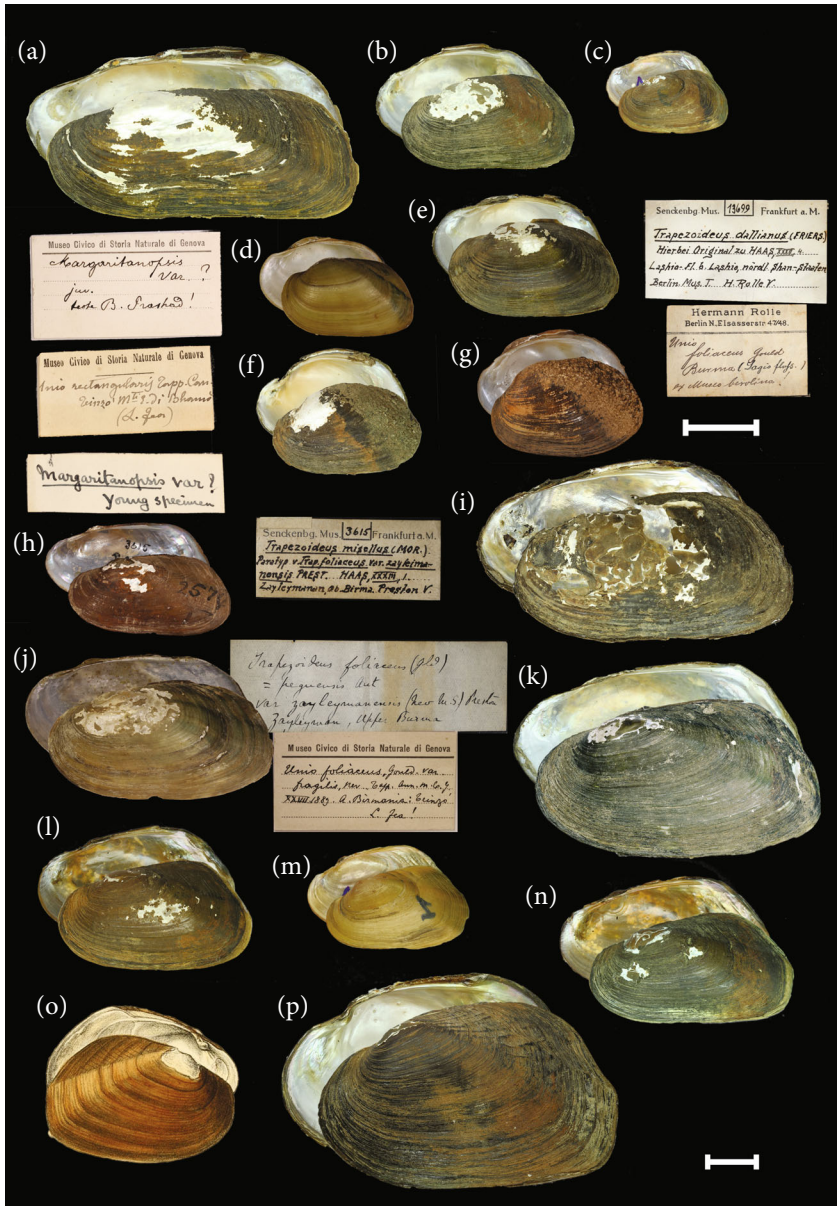

FIGURE 6: Shells of *Yaukthwa*, *Trapezoideus*, and *Pseudodo*n from Myanmar. (a) *Yaukthwa nesemanni* (Konopleva, Bolotov & Kondakov, 2017) (specimen RMBH biv 255/4; Sittaung River). (b) *Yaukthwa nesemanni* (specimen RMBH biv 144/23; Sittaung River). (c) *Yaukthwa nesemanni* (specimen RMBH biv 1022/3; Haungthayaw River). (d) *Unio rectangularis* Tapparone-Canefri, 1889 (=*Yaukthwa rectangularis*) (Tapparone-Canefri's collection; holotype MSNG with its labels; Mole Stream near Teinthaw village, Ayeyarwady Basin). (e) *Yaukthwa rectangularis* [topotype RMBH biv 916/3; Mole Stream, Ayeyarwady Basin). (f) *Yaukthwa dalliana* (Frierson, 1913) (lectotype SMF 13699a; Lashio River near Lashio, Ayeyarwady Basin, northern Shan State, Myanmar). (g) *Yaukthwa dalliana* (topotype RMBH biv 982/2; Lashio River near Lashio, Ayeyarwady Basin). (h) *Yaukthwa zayleymanensis* (Preston, 1912) (syntype SMF 3615; Zayleyman, Upper Burma). (i) *Yaukthwa zayleymanensis* (specimen RMBH biv 679/3; Tarkat Stream, Ayeyarwady Basin). (j) *Unio foliaceus* var. *fragilis* sensu Tapparone-Canefri, 1889 (=*Yaukthwa zayleymanensis*) (Tapparone-Canefri's collection; specimen MSNG with its label; Mole Stream, Ayeyarwady Basin). (k) *Yaukthwa zayleymanensis* (specimen RMBH biv 918/3; Mole Stream, Ayeyarwady Basin). (l) *Trapezoideus mitanensis* sp. nov. (holotype RMBH 1021/1; Mitan Stream, Haungthayaw Basin). (m) *Trapezoideus mitanensis* sp. nov. (paratype RMBH 1022/1; Mitan Stream, Haungthayaw Basin). (n) *Trapezoideus mitanensis* sp. nov. (paratype RMBH 1021/3; Mitan Stream, Haungthayaw Basin). (o) *Pseudodon inoscularis* sensu Hanley & Theobald, 1876 non Gould, 1844 ([8]: pl. IX, image 2). (p) *Pseudodon kayinensis* Bolotov et al., 2020 (RMBH biv 1026/1; Haungthayaw Basin). Scale bar = 2 cm (upper part) and 1 cm (bottom part). No scale for (o) *Pseudodon inoscularis*. Photos: E.S. Konopleva (a–c, e, f, i, k, l–n), I.V. Vikhrev (d, j), and S. Hof (h, g).

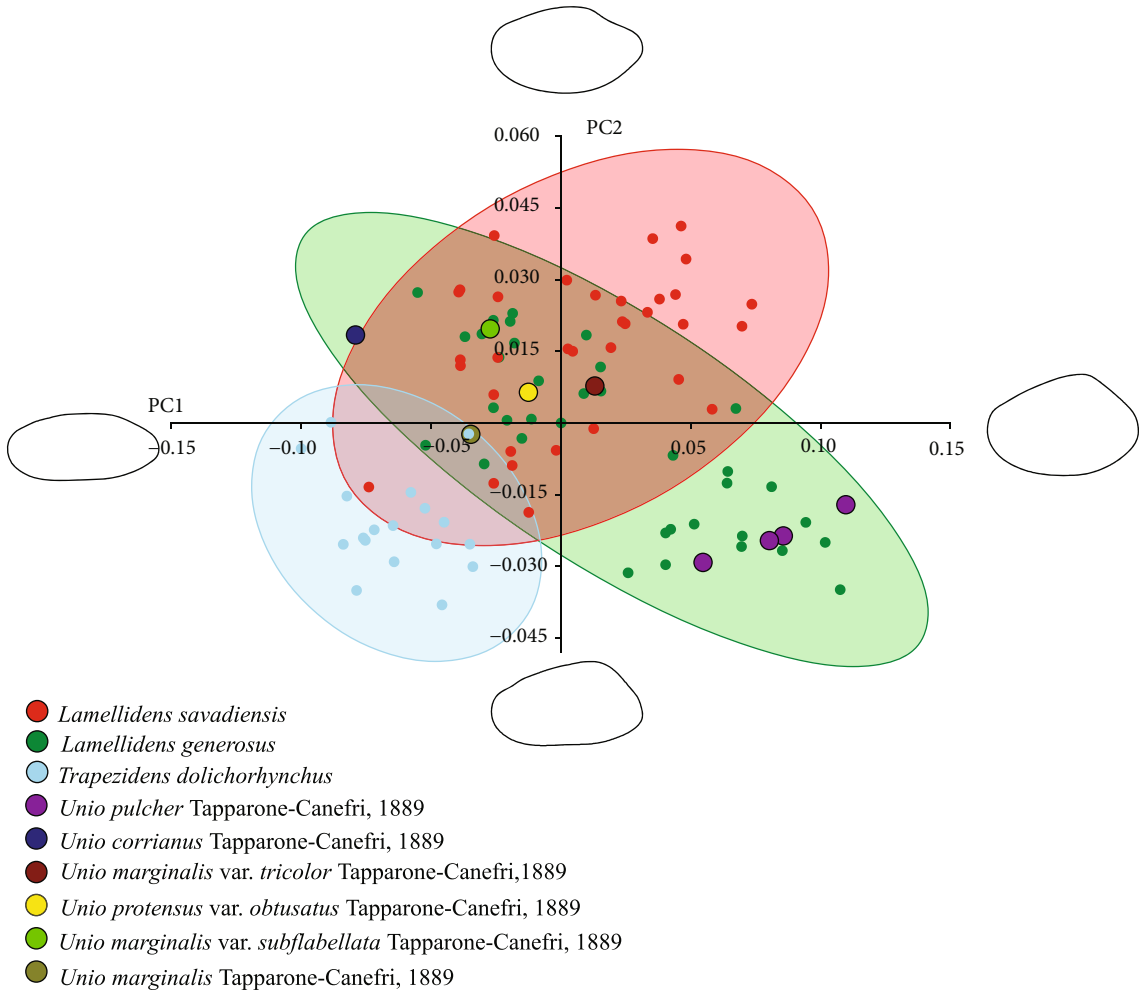

Figure 7: Principal component analysis for the first two PC axes obtained using Fourier coefficients of *Lamellidens* and *Trapezidens* shell shapes. Synthetic shell outlines of the 'extreme' shapes are illustrated with the posterior margin facing to the right and the dorsal margin to the top of the image. The small dots indicate recent samples of *Lamellidens savadiensis* (red dots; $N = 34$), *L. generosus* (green dots; $N = 36$), and *Trapezidens dolichorhynchus* (blue dots; $N = 18$) that were identified on the basis of DNA sequences. The larger multicolor dots indicate the available specimens from Tapparone-Canefri's collection (MSNG). The filled regions show 95% confidence ellipses.

et al., 2020, its sister species (uncorrected *COI* p-distance = 5.4 ± 0.8%) (Table S3).

Prospective topotypes of other nominal Tapparone-Canefri's taxa were also phylogenetically divided among representatives of the Indochinellini, Leoparreysiini, Lamellidentini, and Contradentini (Figure 8, Figures S2–S5).

4. Taxonomic Account: Family Unionidae Rafinesque, 1820

4.1. Genus Indochinella Bolotov, Pfeiffer, Vikhrev & Konopleva, 2018 (Subfamily Parreysiinae Henderson, 1935, Tribe Indochinellini Bolotov, Pfeiffer, Vikhrev & Konopleva, 2018). Type species: *Unio pugio* Benson, 1862 (by original designation).

4.1.1. Indochinella pugio pugio (Benson, 1862). =Unio pugio Benson, 1862: 193 [7]; Tapparone-Canefri, 1889: 344 [15].

=*Oxynaia pugio* (Benson, 1862). – Prashad, 1922: 96 [16].

=*Indochinella pugio* (Benson, 1862). – Bolotov et al., 2018: 6 [18].

=*Indochinella pugio pugio* (Benson, 1862). – Bolotov et al., 2019: 7 [23].

Figures 2(a), 2(b), and 8, Tables 2 and 3, Figure S2.

(1) Type. Whereabouts unknown

(2) Type Locality. "Regione Ava" (Inwa, an ancient town near Mandalay, approx. 21.8609°N, 95.9821°E, Ayeyarwady River, Myanmar) [7].

(3) Topotypes Examined. Myanmar: Sin Khong Stream near Sin Khong village, 22.0632°N, 96.0810°E, Mandalay, Ayeyarwady River basin, 04.iii.2018, 3 specimens (RMBH biv 441), Bolotov, Vikhrev and Nyein Chan leg (Figure 2(a)).

(4) Tapparone-Canefri's Material Examined. One shell in MSNG labelled "Mandalay, del mercato. Leg. L. Fea!" (Mandalay market, Myanmar) (Figure 2(b)).

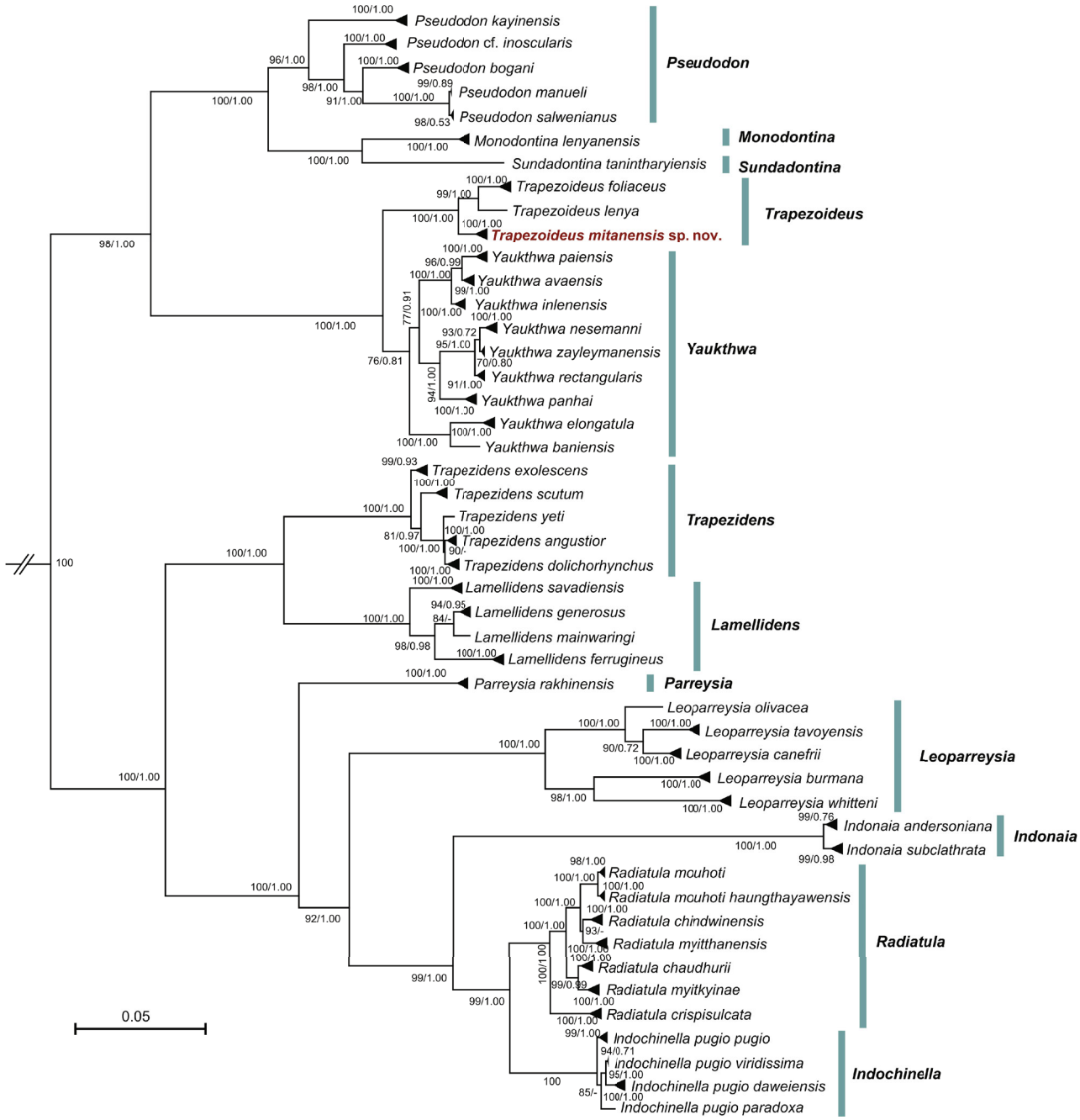

Figure 8: Maximum likelihood phylogeny of the complete data set of mitochondrial and nuclear sequences (five partitions: three codons of *COI*+16*S rRNA*+28*S rRNA*) of the Unionidae from Myanmar. Scale bar indicates the branch lengths. Black numbers near nodes are ML ultrafast bootstrap support values (BS)/Bayesian Posterior Probabilities (BPP). The new species name is red. Outgroup is not shown.

(5) Other Material Examined. Myanmar: Ayeyarwady River near Tha Phan Kone village, 21.2566°N, 94.9848°E, Ayeyarwady Basin, 02.iii.2018, 3 specimens (RMBH biv 426), Bolotov, Vikhrev, and Nyein Chan leg.; ox-bow lake near Ta Naung Taig village, 21.4064°N, 95.3399°E, Mandalay Region, Ayeyarwady Basin, 03.iii.2018, 3 specimens (RMBH biv 428A), Bolotov, Vikhrev, and Nyein Chan leg.; Nam Pha Lake near Bhamo, 24.2972°N, 97.2610°E, Kachin State, Ayeyarwady Basin, 29.xi.2016, 3 specimens (RMBH biv 258, including biv 258/1 and 258/2 sequenced), Vikhrev and Nyein Chan leg.; Myaung Lake near Bhamo and Tha Pya Khone village, 24.2387°N, 97.1658°E, Kachin State, Ayeyarwady Basin, 01.xii.2016, 7 specimens (RMBH biv 268, including biv 268/1, biv 268/2 and biv 268/4 sequenced), Vikhrev and Nyein Chan leg.; ox-bow lake near Dagaung city, 23.5153°N, 96.0170°E, Kachin State, Ayeyarwady Basin, 11.ii.2017, 7 specimens (RMBH biv 327), Nyen Chan leg.; Ayeyarwady River, 24.2965°N, 96.4746°E, Kachin State, Ayeyarwady Basin, 10.ii.2017, 7 specimens (RMBH biv 332), Nyen

Chan leg.; Pathein River, 17.4567°N, 95.0086°E, Ayeyarwady Basin, 01.xii.2018, 3 specimens (RMBH biv 651, ethanol-preserved tissue snips only), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg.; Mole Stream, 24.4010°N, 97.2543°E, Ayeyarwady Basin, 11.iii.2020, 6 specimens (RMBH biv 919), Nyein Chan leg.

(6) Distribution. Ayeyarwady Basin in Myanmar [18, 23].

(7) Comments. The *Indochinella pugio* group has been revised with a description of three novel allopatric geographic races in addition to the nominative subspecies [23]. However, this group needs future research, because these subspecies may actually represent species-level taxa. *Indochinella pugio pugio* is a common mussel throughout the Ayeyarwady Basin, including the main channel of the river [23].

4.1.2. Indochinella pugio paradoxa Bolotov et al., 2019. =*Unio crispatus* Tapparone-Canefri, 1889: 343 [15] (identification error).

=*Indonaia crispata* Prashad, 1922: 95 [16] (identification error).

=*Indochinella pugio paradoxa* Bolotov et al., 2019: 7 [23]. Figures 2(c) and 8, Tables 2 and 3, Figure S2.

(1) Type. Holotype RMBH biv 361/1 labelled "Myanmar: Haungthayaw River upstream of Kawkareik town, 16.47144°N, 98.21825°E, 9.ii.2018, Nyein Chan leg." (RMBH).

(2) Type Locality. Haungthayaw River upstream of Kawkareik town, 16.4714°N, 98.2182°E, Myanmar [23].

(3) Type Material Examined. Myanmar: The type series of *Indochinella pugio paradoxa* from the Haungthayaw River, 09.ii.2018, 9 specimens (RMBH biv 361: holotype biv 361/1; paratypes: biv 361/2, biv 361/3, biv 361/4, biv 361/5, biv 361/6, biv 361/7, biv 361/8, and biv 361/9), Nyein Chan leg.

(4) Tapparone-Canefri's Material Examined. The specimens were not found in the MSNG

(5) Distribution. Haungthayaw Basin, southeastern Myanmar. There are also some specimens from the nearest Ataran and Hlaingbwe basins

(6) Comments. Conchologically, this subspecies clearly resembles taxa of the genus *Scabies*, e.g. *S. crispata* (Gould, 1843), by having green zigzag ridges over the shell [23]. We think that the incorrect identification of the Haungthayaw *Indochinella* population as *Scabies crispata* made by Tapparone-Canefri [15] and Prashad [16] was biased by the convergent external resemblance of these taxa.

4.2. Genus Indonaia Prashad, 1918 (Subfamily Parreysiinae Henderson, 1935, Tribe Indochinellini Bolotov, Pfeiffer, Vikhrev & Konopleva, 2018). Type species: *Unio caeruleus* Lea, 1831 (by original designation).

4.2.1. Indonaia andersoniana (Nevill, 1877). =*Unio andersoniana* Nevill, 1877: 40 [10].

=*Unio coeruleus* Tapparone-Canefri, 1889: 344 [15] (identification error) (Figures 2(d)–2(f), and 2(h)).

=*Unio marginalis* var. *bilineata* Tapparone-Canefri, 1889: 347 [15] (identification error) (Figures 2(g) and 2(i)).

=*Unio smaragdites* Tapparone-Canefri, 1889: 343 [15] (this shell is labelled "*Unio scobinatus* Bens.??" in MSNG; identification error) (Figures 2(j) and 2(k)).

=*Parreyssia smaragdites* Prashad, 1922: 102 [16] (identification error).

=*Unio andersoni* Ramakrishna et al., 2004: 79 [49] (incorrect spelling for *Unio andersoniana* Nevill, 1877).

=*Parreysia* (*Radiatula*) *andersoni* Ramakrishna et al., 2004: 79 [49] (incorrect spelling for *Unio andersoniana* Nevill, 1877).

=*Indonaia andersoniana* (Nevill, 1877). – Bolotov et al., 2017: 10 [24].

=*Unio leioma* Tapparone-Canefri, 1889: 344 [15] (Figures 2(l) and 2(m)).

Figures 2(d)–2(m), and 8, Tables 2 and 3, Figure S2.

(1) Type. Syntypes ZSI M5192/1 (3 complete shells and one separate valve) labelled "Myadong, Upper Burma. J. Anderson", Zoological Survey of India, Kolkata, India [49].

(2) Type Locality. Myadoung, Upper Burma (Ayeyarwady River near Mya Taung village, 23.7310°N, 96.1486°E, Myanmar) [10].

(3) Topotypes Examined. Myanmar: Nant Phar Lake near Bhamo, 24.2972°N, 97.2610°E, Kachin State, Ayeyarwady Basin, 29.xi.2016, 4 specimens (RMBH biv 259, including biv 259/1, 259/3 and 259/4 sequenced), Vikhrev and Nyein Chan leg.; Nant Sa Yi River near Bhamo, 24.2196°N, 97.2224°E, Kachin State, Ayeyarwady Basin, 30.xi.2016, 3 specimens (RMBH biv 263, including biv 263/1 and biv 263/2 sequenced), Vikhrev and Nyein Chan leg.; Myaung Lake near Bhamo, 24.2387°N, 97.1658°E, Kachin State, Ayeyarwady Basin, 01.xii.2016, 3 specimens (RMBH biv 267, including biv 267/1 and biv 267/3 sequenced), Vikhrev and Nyein Chan leg.

(4) Tapparone-Canefri's Material and Recent Samples Examined. Two shells and two valves in MSNG labelled "*Unio coeruleus* Lea. Tapp. Ann. M. C. Gen. XXVII. 1889, p. 344. Mandalay, del mercato. Dic(embre). 1885. L. Fea!"; one shell labelled "*Unio marginalis* Lk. var. *bilineata* Hanl. & Theob. Tapp. Ann. M. C. Gen. XXVII. 1889, p. 347. Mandalay, del mercato. Dic(embre). 1885 – Genn(aio). 1886. L. Fea!". One shell in MSNG labelled "*Unio scobinatus* Bens.?? Det. Tapp. Mandalay, del mercato. Dic(embre). 1885 – Genn(aio). 1886. L. Fea!". Recent samples from Fea's locality: Ayeyarwady River near Mandalay, 21.8893°N, 95.9978°E, Ayeyarwady Basin, 03.iii.2018, 3 specimens (RMBH biv 450, including biv 450/1 and biv 450/2 sequenced), Bolotov,

Vikhrev, and Nyein Chan leg. (Figures 2(j) and 2(k)); ox-bow lake near Ta Naung Taig village, 21.4064°N, 95.3399°E, 03.iii.2018, Ayeyarwady Basin, 3 specimens (RMBH biv 429, including biv 429/1, biv 429/2 and biv 429/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg (Figures 2(d)–2(i)).

(5) Other Material Examined. Myanmar: Indawgyi Lake, 25.1099°N, 96.2925°E, Ayeyarwady Basin, 25.iii.2014, 3 specimens (RMBH biv 108, including biv 108/1, biv 108/2 and biv 108/3 sequenced), Bolotov and Vikhrev leg.; Mizan Stream, 16.9770°N, 97.6330°E, Salween Basin, 11.ii.2018, 3 specimens (RMBH biv 368, including biv 368/1, biv 368/2 and biv 368/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Bago River, 17.5334°N, 96.3315°E, 18.ii.2018, 15 specimens (RMBH biv 383, including biv 383/1, biv 383/2 and biv 383/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Bago River, 17.6795°N, 96.2346°E, 19.ii.2018, 3 specimens (RMBH biv 389, including biv 389/1, biv 389/2 and biv 389/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Balu River near Loikaw, 19.6682°N, 97.1848°E, Salween Basin, 25.ii.2018, 5 specimens (RMBH biv 405A, including biv 405A/1, biv 405A/2 and biv 405A/3 sequenced; RMBH biv 407A, including biv 407A/1 and biv 407A/2 sequenced), local fishermen leg.; Hnit Saung Pyang Stream, 19.514021°N, 96.262109°E, Sittaung Basin, 8 specimens (RMBH biv 407, including biv 407/1, biv 407/2 and biv 407/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Sin Thay Stream, 20.1533°N, 96.1267°E, Sittaung Basin, 01.iii.2018, 4 specimens (RMBH biv 412, including biv 412/1, biv 412/2 and biv 412/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Mone Ding Dam outlet, 20.8099°N, 95.7242°E, Ayeyarwady Basin, 01.iii.2018, 3 specimens (RMBH biv 414, including biv 414/1, biv 414/2 and biv 414/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Ayeyarwady River near Mandalay, 21.9574°N, 96.0510°E, Ayeyarwady Basin, 03.iii.2018, 1 specimen (RMBH biv 434, sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Sin Khong Stream, 22.0632°N, 96.0810°E, Ayeyarwady Basin, 04.iii.2018, 1 specimen (RMBH biv 440), Bolotov, Vikhrev, and Nyein Chan leg.; Indaw River near Sell Ywar village, 24.2123°N, 96.0819°E, Ayeyarwady Basin, 14.xi.2018, 3 specimens (RMBH biv 615, including biv 615/1 and biv 615/2 sequenced), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg; Bago River, 18.0791°N, 96.0449°E, 24.iii.2020, 4 specimens (RMBH biv 1005, including biv 1005/1, biv 1005/2 and biv 1005/3 sequenced), Bolotov, Vikhrev, Nyein Chan, Kondakov, and Gofarov leg.

(6) Distribution. Ayeyarwady, Bago, and Salween basins, Myanmar [27].

(7) Comments. This conchologically variable species is widespread and generally common throughout the Ayeyarwady and Bago basins [27].

4.3. Genus Radiatula Simpson, 1900 (Subfamily Parreysiinae Henderson, 1935, Tribe Indochinellini Bolotov, Pfeiffer, Vikhrev & Konopleva, 2018). Type species: *Unio crispisulcatus* Benson, 1862 (by original designation).

4.3.1. Radiatula chaudhurii (Preston, 1912). =Unio burmanus Tapparone-Canefri, 1889: 349 [15] (identification error) (Figures 2(n)–2(p)).

=*Nodularia* (s. str.) *chaudhurii* Preston, 1912: 290 [50]; Ramakrishna et al., 2004: 47 [49].

=*Radiatula* aff. *bonneaudii* sp.1 Bolotov et al., 2017: 10 [24] (preliminary identification).

=*Radiatula chaudhurii* (Preston, 1912). – Bolotov et al., 2019: 5 [23].

Figures 2(n)–2(p), and 8, Tables 2 and 3, Figure S2.

(1) Type. Holotype M 2545/1 labelled "Upper Burma", Zoological Survey of India, Kolkata, India [49].

(2) Type Locality. Upper Burma [50].

(3) Topotypes Examined. Myanmar: Shweli River, 24.0171°N, 96.4729°E, Ayeyarwady Basin, 10.iii.2020, 10 specimens (RMBH biv 913, including biv 913/1, biv 913/2 and biv 913/3 sequenced), Bolotov and Vikhrev leg

(4) Tapparone-Canefri's Material and Recent Sample Examined. One shell in MSNG labelled "*Unio burmanus* Blanf. Tapp. Ann. M. C. G. XXVII, 1889, p. 349. Alta Birmania: Teinzo del Mule Chaung – Marz. 1886. L. Fea!" (Mole Stream near Teinthaw village, 24.3978°N, 97.2519°E, Ayeyarwady Basin, Myanmar). Recent sample from Fea's locality: Mole Stream, 24.401°N, 97.2544°E, Ayeyarwady Basin, 11.iii.2020, 14 specimens (RMBH biv 920 and biv 921, including biv 920/1, biv 920/2, biv 920/3, biv 921/1, biv 921/2 and biv 921/3 sequenced), Nyein Chan leg. (Figures 2(n)–2(p)).

(5) Other Material Examined. Myanmar: Tar Pein River, 24.3049°N, 97.2514°E, Ayeyarwady Basin, 29.xi.2016, 10 specimens (RMBH biv 260, including biv 260/5, biv 260/9 and biv 260/10 sequenced), Vikhrev and Nyein Chan leg.; Ayeyarwady River, 21.3145°N, 95.0589°E, 02.iii.2018, 10 specimens (RMBH biv 421, including biv 421/2 and biv 421/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Ayeyarwady River, 21.2566°N, 94.9848°E, 02.iii.2018, 11 specimens (RMBH biv 427, including biv 427/1 and biv 427/2 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Indaw Lake, 24.2665°N, 96.1228°E, Ayeyarwady Basin, 13.xi.2018, 30 specimens (RMBH biv 604, biv 605 and biv 606, including biv 604/1, biv 604/2, biv 605/1, biv 605/2, biv 605/3, biv 606/1 and 606/2 sequenced), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg.; Nant Poat Kalay River, 24.2130°N, 96.1089°E, Ayeyarwady Basin, 13.xi.2018, 11 specimens (RMBH biv 610 and biv 611, including biv 610/1 biv 610/2, biv 611/1 and biv 611/2 sequenced), Bolotov, Vikhrev, Lopes-Lima, Bogan,

and Nyein Chan leg.; Indaw river, 24.2123°N, 96.0819°E, Ayeyarwady Basin, 14.xi.2018, 5 specimens (RMBH biv 614, including biv 614/1 and biv 614/2 sequenced), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg.

(6) Distribution. Ayeyarwady Basin, Myanmar.

(7) Comments. The shell shape of this species varies in a broad range from ovate to almost triangular. The Mole Stream's sample shares a thick, short, triangular *Leoparreysia*-like shell morphotype that was also recorded from several other localities (e.g., the Indaw Lake).

4.3.2. Radiatula mouhoti haungthayawensis Bolotov et al., 2019. =*Unio bonneaudii* Tapparone-Canefri, 1889: 343 [15] (identification error).

=*Indonaia bonneaudi* Prashad, 1922: 94 [16].

=*Radiatula mouhoti haungthayawensis* Bolotov et al., 2019: 5 [23].

Figures 2(q) and 8, Tables 2 and 3, Figure S2.

(1) Type. Holotype RMBH biv360/1 labelled "Myanmar: Haungthayaw River upstream of Kawkareik town, 16.4714°N, 98.2183°E, 9.ii.2018, Nyein Chan leg." (RMBH).

(2) Type Locality. Haungthayaw River upstream of Kawkareik town, 16.4714°N, 98.2182°E, Myanmar.

(3) Type Material Examined. The type series of *Radiatula mouhoti haungthayawensis* (RMBH biv 360) [23].

(4) Tapparone-Canefri's Material and Recent Sample Examined. The specimens were not found in the MSNG. Recent sample from Fea's locality: Myanmar: Mitan Stream, 16.0019°N, 98.4064°E, Haungthayaw Basin, 16.ii.2020, 10 specimens (RMBH biv 1023, including biv 1023/1, biv 1023/2 and biv 1023/3 sequenced), Than Win leg.

(5) Distribution. Haungthayaw Basin, southeastern Myanmar.

(6) Comments. The species is conchologically similar to *Radiatula chaudhurii* (Preston, 1912) and *Indonaia bonneaudii* (Eydoux, 1838).

4.4. Genus Leoparreysia Vikhrev, Bolotov & Aksenova, 2017 (Subfamily Parreysiinae Henderson, 1935, Tribe Leoparreysiini Vikhrev, Bolotov & Kondakov, 2017). Type species: *Leoparreysia canefrii* Vikhrev, Bolotov & Kondakov, 2017 (by original designation).

4.4.1. Leoparreysia tavoyensis (Gould, 1843). =Unio tavoyensis Gould, 1843: 140 [1].

=*Unio luteus* Lea, 1856: 93 [51]; Lea, 1857: 291 [52] (new junior synonym).

=*Unio parma* Sowerby, 1868: pl. 95, sp. 514 [11]; Tapparone-Canefri, 1889: 339 [15].

=*Unio bhamoensis* Theobald, 1873: 207 [13] (new junior synonym).

=*Unio mandelayensis* Theobald, 1873: 208 [13] (new junior synonym); Tapparone-Canefri, 1889: 342 [15].

=*Unio feae* Tapparone-Canefri, 1889: 340 [15] (new junior synonym).

=*Unio houngdarauicus* Tapparone-Canefri, 1889: 341 [15] (new junior synonym).

=*Parreysia choprae* Prashad, 1930: 248 [53] (new junior synonym).

=*Parreyssia bhamoensis* (Theobald, 1873). – Prashad, 1922: 100 [16].

=*Parreyssia houngdaranicus* Prashad, 1922 [16]: 101 (incorrect spelling of *Unio houngdarauicus* Tapparone-Canefri, 1889).

=*Parreyssia tavoyensis* (Gould, 1843). – Prashad, 1922: 104 [16].

=*Parreyssia feae* (Tapparone-Canefri, 1889). – Prashad, 1922: 105 [16].

=*Leoparreysia bhamoensis* (Theobald, 1873). – Bolotov et al., 2017: 10 [24].

=*Leoparreysia feae* (Tapparone Canefri, 1889). – Bolotov et al., 2017: 10 [24].

=*Leoparreysia houngdarauica* (Tapparone Canefri, 1889). – Bolotov et al., 2017: 10 [24].

=*Leoparreysia tavoyensis* (Gould, 1843). – Bolotov et al., 2017: 10 [24].

Figures 3 and 8, Tables 2 and 3, Figure S3.

(1) Type. Syntype MCZ 169389 labelled "Tavoy, British Burmah. F. Mason" (MCZ) (Figure 3(a)).

(2) Type Locality. Tavoy, British Burmah (Dawei River, approx. 14.5014°N, 98.1558°E, Myanmar).

(3) Topotypes Examined. Myanmar: Dawei River, 14.5013° N, 98.1558°E, 26.iv.2015, 1 specimen (RMBH biv 149 sequenced), Bolotov and Vikhrev leg. (Figure 3(b)).

(4) Additional Type and Topotype Material Examined. *Unio luteus* Lea, 1856: holotype AMNH 29109. Type locality: Newville Burmah (Hlaingbwe River near the former Newville village, 16.9834°N, 97.9043°E, Myanmar). Topotypes examined: Hlaingbwe River, 4 specimens (RMBH biv 641A, only dry shells), Than Win leg. (Figure 3(c)).

Unio parma Sowerby, 1868: holotype NHMUK 88-12-4-1669. Type locality: Tennasserim, E. Indies (Tenasserim, Myanmar). Topotypes examined: Myanmar: Tanintharyi River, 12.2523°N, 99.0402°E, 26.xi.2018, 7 specimens (RMBH biv 634, including biv 634/1, biv 634/2 and biv 634/3 sequenced), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg. (Figure 3(d)).

Unio bhamoensis Theobald, 1873: syntype NHMUK 88-12-4-1672. Type locality: prope Bhamo Birmanico; necnon in Prome occidental Provinciá Pegu (Bhamo, Ayeyarwady Basin, Myanmar). Topotypes examined: Myanmar: Myaung Lake near Bhamo, 24.2387°N, 97.1658°E, Ayeyarwady Basin,

01.xii.2016, 11 specimens (RMBH biv 266, including biv 266/4, biv 266/5 and biv 266/6 sequenced), Vikhrev and Nyein Chan leg. (Figure 3(f)).

Unio mandelayensis Theobald, 1873: syntype NHMUK 1888-12-4-2018. Type locality: prope Mandelay, regno Birmanico (Mandalay, Ayeyarwady Basin, Myanmar). Topotypes examined: Myanmar: Ayeyarwady River, 21.8893°N, 95.9978°E, Mandalay, 04.iii.2018, 2 specimens (RNBH biv 447, including biv 447/1 and biv 447/2 sequenced), Bolotov, Vikhrev, and Nyein Chan leg. (Figure 3(g)).

Unio feae Tapparone-Canefri, 1889: syntypes ZSI M11965/2 (note on the label: Exchange from Geneva Mus.) and ZSI M17512 (Figure 3(h)), syntypes MNHN-IM-2000-38002, MNHN-IM-2000-38003, MNHN-IM-2000-38004 and MNHN-IM-2000-38005. Type locality: Meetan, fiume Houngdarau (Mitan Stream, Haungthayaw River, Myanmar). Topotypes examined: Myanmar: Haungthayaw River upstream of Kawkareik town, 16.4714°N, 98.2183°E, 09.ii.2018, 1 specimen (RMBH biv 362/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg. (Figure 3(i)).

Unio houngdarauicus Tapparone-Canefri, 1889: syntypes MNHN-IM-2000-37124. Type locality: Meetan, fiume Houngdarau (Mitan Stream, Haungthayaw River, Myanmar). Topotypes examined: Myanmar: Haungthayaw River upstream of Kawkareik town, 16.4714°N, 98.2183°E, 09.ii.2018, 1 specimen (RMBH biv 362/2, sequenced), Nyein Chan leg. (Figure 3(j)).

Parreysia choprae Prashad, 1930: holotype ZSI M13018/2 (Figure 3(e)). Type locality: Bank of a hill-stream about 5 miles from Hopin towards Namna, Myitkyina (a stream about 5 miles from Hopin towards Namna, 25.0352°N, 96.5885°E, Ayeyarwady Basin, Myitkyina District, Myanmar).

(5) Other Material Examined. Myanmar: Mizan Stream, 16.9770°N, 97.6330°E, Salween Basin, 11.ii.2018, 18 specimens (RMBH biv 367, including biv 367/1, biv 367/2 and biv 367/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Ayeyarwady River near Tha Phan Kone village, 21.2566°N, 94.9848°E, 02.iii.2018, 11 specimens (RMBH biv 425, including biv 425/1 and biv 425/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Tanintharyi River, 12.0914°N, 99.0174°E, 26.xi.2018, 3 specimens (RMBH biv 635, including biv 635/1, biv 635/2 and biv 635/3 sequenced), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg.; Nga Wun Stream, 11.8233°N, 99.1493°E, 2018, Tanintharyi Basin, 3 specimens (RMBH biv 646, including biv 646/2 sequenced), Nyein Chan leg.

(6) Distribution. This species is widespread throughout Myanmar, and it was recorded in the following rivers: Ayeyarwady, Salween, Hlaingbwe, Haungthayaw, Dawei (former Tavoy), and Tanintharyi (former Great Tenasserim). There are no recent samples from the Bago (former Pegu) River.

(7) Comments. This seems to be one of the most widespread and conchologically variable freshwater mussel species in Myanmar, and its populations from different rivers were described as separate nominal species: *Unio tavoyensis* (Dawei River), *U. bhamoensis* syn. nov. and *U. mandelayensis* syn. nov. (Ayeyarwady River), *U. feae* syn. nov. and *U. houngdarauicus* syn. nov. (Haungthayaw River), *U. parma* (Tanintharyi River), and *U. luteus* syn. nov. (Hlaingbwe River). The nominal taxon *Parreysia choprae* syn. nov. (Ayeyarwady River) also represents a conchological variety of *Leoparreysia tavoyensis*.

4.5. Genus Lamellidens Simpson, 1900 (Subfamily Parreysiinae Henderson, 1935, Tribe Lamellidentini Modell, 1942). Type species: *Unio marginalis* Lamarck, 1819 (by original designation).

4.5.1. Lamellidens generosus (Gould, 1847). =Unio generosus Gould, 1847: 220 [3] (Figure 4(c)).

=*Unio marginalis* var. *zonata* Tapparone-Canefri, 1889: 346 [15] (Figure 4(d)).

=*Unio pulcher* Tapparone-Canefri, 1889: 350 [15] (primary homonym of *Unio pulcher* Lea, 1838; renamed *Lamellidens burmanus* Simpson, 1914). (Figures 4(a) and 4(b)).

=*Unio pulcher* var. *lamellatiformis* Tapparone-Canefri, 1889: 351 [15].

=*Unio pulcher* var. *ponderosulus* Tapparone-Canefri, 1889: 351 [15].

=*Unio generosus* var. *delapsus* Tapparone-Canefri, 1889: 352 [15].

=*Lamellidens burmanus* Simpson, 1914: 1170 [54] (replacement name for *Unio pulcher* Tapparone-Canefri, 1889).

=*Unio protensus* var. *obtusatus* Tapparone-Canefri, 1889: 350 [15] (new junior synonym) (Figures 4(e) and 4(d)).

=*Unio corrianus* Tapparone-Canefri, 1889: 347 [15] (Figures 4(g) and 4(h)).

=*Unio marginalis* var. *obesa* Hanley & Theobald, 1872: 20 [55] (unavailable name: junior homonim of *Unio obesus* Lea, 1831).

=*Trapezidens obesa* (Hanley & Theobald, 1876). – Bolotov et al., 2017: 10 [24].

Figures 4, 7, and 8, Tables 2 and 3, Figures S1 and S4.

(1) Type. Syntype MCZ 169449.

(2) Type Locality. Newville, Tavoy, British Burmah (Hlaingbwe River near the former Newville village, 16.9834°N, 97.9043°E, Myanmar).

(3) Topotype Examined. Hlaingbwe River, 17.0292°N, 97.8099°E, 2018, 3 specimens (RMBH biv 636, including biv 636/1, biv 636/2 and biv 636/3 sequenced), Than Win leg. (Figure 4(c)).

(4) Tapparone-Canefri's Type Material and Recent Topotypes Examined. *Unio pulcher* Tapparone-Canefri, 1889: Four syntypes in MSNG labelled "*Unio pulcher*, Tapp. Can. Ann. M. C. Gen. XXVII, 1889, p. 350. Typus! Tenasserim: Meetan, del fiume Houngdarau, marzo 1887. Leg. L. Fea!" and "*Lamellidens generosus* (Gould), detto B. Prashad". Type

locality: Meetan, fiume Houngdarau (Mitan Stream, Haungthayaw River, Myanmar). Topotype material examined: Myanmar: Haungthayaw River, 15.962°N, 98.4152°E, 16.ii.2020, 10 specimens (RMBH biv 1024, including biv 1024/1, biv 1024/2 and biv 1024/3 sequenced), Than Win leg. (Figures 4(a) and 4(b)).

Unio protensus var. *obtusatus* Tapparone-Canefri, 1889: Holotype (by original designation) in MSNG labelled "*Unio protensus* Tapp. var. *obtusatus*, Tapp. Ann. M. C. Gen. XXVII, 1889, p. 350 (Tipo della var.!). Bassa Birmania: Prome, negli bagni della città, marzo 1886. Leg. L. Fea!" and "*Lamellidens marginalis* (Lam.), detto B. Prashad". Type locality: Prome, Bassa Birmania (Irrawaddy near Pyay city, approx. 18.8387° N, 95.2206°E). Topotype material examined: Myanmar: Nga Wun river near Pyay city, 18.8624° N, 95.2822°E, Ayeyarwady Basin, 11.xii.2018, 10 specimens (RMBH biv 672, including biv 672/1 and biv 672/2 sequenced), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg. (Figures 4(e) and 4(f)).

(5) Tapparone-Canefri's Non-Type Material Examined. One shell in MSNG labelled "*Unio corrianus*, Lea. Tapp. Ann. M. C. Gen. XXVII, 1889, p. 347. Mandalay, del mercato. Dic(embre). 1885 – Genn(aio). 1886. Leg. L. Fea!". Two shells of *Lamellidens* sp. in MSNG without label data (Figures 4(g) and 4(h)).

(6) Other Material Examined. Myanmar: Pathi River, 19.0278°N, 96.5353°E, Sittaung Basin, 23.xi.2016, 1 specimen (RMBH biv 242/3 sequenced), Vikhrev and Nyein Chan leg.; Pathi River, 19.0278°N, 96.5353°E, Sittaung Basin, 23.xi.2016, 17 specimens (RMBH biv 243, including biv 243/10, biv 243/12 and biv 243/14 sequenced), Vikhrev and Nyein Chan leg.; reservoir on the Yetho River, 18.8457°N, 96.3012°E, Sittaung Basin, 24.xi.2016, 7 specimens (RMBH biv 244, including biv 244/2, biv 244/3 and biv 244/5 sequenced), Vikhrev and Nyein Chan leg.; fish pond near Taungoo, 18.9593°N, 96.4831°E, Sittaung Basin, 25.xi.2016, 1 specimen (RMBH biv 247/10 sequenced), Vikhrev and Nyein Chan leg.; Myit Kyi Pauk Stream, 18.9613°N, 96.4455°E, Sittaung Basin, 26.xi.2016, 1 specimen (RMBH biv 250/10 sequenced), Vikhrev and Nyein Chan leg.; Kalemyo market, 23.1746°N, 94.0423°E, Ayeyarwady Basin, 04.ii.2018, 11 specimens (RMBH biv 355, including biv 355/1, biv 355/2 and biv 355/3 sequenced), bought on the local market; a fish pond near Kalemyo, 23.1746°N, 94.0423°E, Chindwin River, Ayeyarwady Basin, 04.ii.2018, 10 specimens (RMBH biv 356, including biv 356/1, biv 356/2 and biv 356/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; tributary of Nayintaya River near Thayagon village, 23.4160°N, 94.0875°E, Chindwin River, Ayeyarwady Basin, 04.ii.2018, 5 specimens (RMBH biv 358, including biv 358/1, biv 358/2 and biv 358/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; tributary of Haungthayaw River, 16.6104°N, 98.0110°E, 09.ii.2018, 5 specimens (RMBH biv 359, including biv 359/1 and biv 359/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Haungthayaw River, 16.4714°N, 98.2183°E, upstream of Kawkareik town, 09.ii.2018, 16 specimens (RMBH biv 363, including biv 363/1, biv 363/2 and biv 363/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; stream near the Kawkareik town, 16.5365°N, 98.2202°E, Haungthayaw Basin, 09.ii.2018, 7 specimens (RMBH biv 364, including biv 364/1 and biv 364/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; ox-bow lake south of Hpa-An airport, 16.8819°N, 97.6629°E, Salween Basin, 09.ii.2018, 5 specimens (RMBH biv 365, including biv 365/1 and biv 365/2 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Mizan Stream, 16.9770°N, 97.6330°E, Salween Basin, 11.ii.2018, 7 specimens (RMBH biv 366, including biv 366/2 and biv 366/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Shwe Laung lake, 17.4395°N, 97.2457°E, Bilin Basin, 13.ii.2018, 12 specimens (RMBH biv 372, including biv 372/1, biv 372/2 and biv 372/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Bago - Sittaung channel, 17.5818°N, 96.7733°E, 16.ii.2018, 12 specimens (RMBH biv 376, including biv 376/1, biv 376/2 and biv 376/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Moeyungyi Lake, 17.5968°N, 96.5950°E, 17.ii.2018, 10 speciemens (RMBH biv 378, including biv 378/1, biv 378/2 and biv 378/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; pond near the Salu Dam, 17.5492°N, 96.3736°E, Bago Basin, 18.ii.2018, 10 specimens (RMBH biv 379, including biv 379/1, biv 379/2 and biv 379/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Bago river, 17.5334°N, 96.3315°E, 18.ii.2018, 5 specimens (RMBH biv 384, including biv 384/1, biv 384/2 and biv 384/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Moload Stream, 17.6011°N, 96.2861°E, Bago Basin, 18.ii.2018, 2 specimens (RMBH biv 385/2 and biv 385/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Kyauk Phar Stream, 17.6660°N, 96.2465°E, Bago Basin, 19.ii.2018, 2 specimens (RMBH biv 387/1 and biv 387/2 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Pagaing Stream, 17.7080°N, 96.7155°E, Bago Basin, 20.ii.2018, 10 specimens (RMBH biv 392, including biv 392/1, biv 392/2 and biv 392/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg; Winyaw river, 15.6685°N, 97.9496°E, Ataran Basin, 20.xi.2018, 10 specimens (RMBH biv 621), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg.; Pathein river, 17.4567°N, 95.0086°E, Ayeyarwady Basin, 01.xii.2018, 2 specimens (RMBH biv 648 (only snips), all sequenced), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg.

(7) Distribution. Endemic to Myanmar: widespread throughout the Ayeyarwady (including Chindwin), Bago, Sittaung, Lower Salween, Haungthayaw, Hlaingbwe, and Ataran basins.

(8) Comments. Bolotov et al. [24] applied the name *Lamellidens generosus* to a lineage endemic to the Inle Lake drainage, Salween River basin. This taxonomic hypothesis was based on their data on the single-drainage pattern of freshwater mussel endemism throughout Myanmar. However, the number of single-drainage endemic species in the country was overestimated due to the limited coverage of river basins by sampling efforts [21]. It was found that Lake Inle and surrounding waters are inhabited by other species, *Lamellidens ferrugineus* (Annandale, 1918) (=*Physunio micropteroides* Annandale, 1918) [56]. In turn, *Unio pulcher* var. *lamellatiformis, U. pulcher* var. *ponderosulus*, and *U. generosus* var. *delapsus* described from Mitan Stream, Haungthayaw River most likely represent conchological varieties of *Lamellidens generosus* based on the original description, shell proportions, and geographic evidence.

4.5.2. Lamellidens savadiensis (Nevill, 1877). =Unio marginalis var. savadiensis Nevill, 1877: 37 [10] (Figure 5(a)).

= *Unio marginalis* var. *cylindrica* Hanley & Theobald, 1872: 20 [55] (Figures 5(b) and 5(c)).

=*Unio marginalis* var. *subflabellata* Tapparone-Canefri, 1889: 346 [15] (new junior synonym) (Figures 5(e), 5(g), and 5(h)).

=*Unio marginalis* var. *tricolor* Tapparone-Canefri, 1889: 347 [15] (identification error) (Figures 5(d) and 5(f)).

Figures 5(a)–5(h), 7, and 8, Tables 2 and 3, Figures S1 and S4.

(1) Type. Not traced.

(2) Type Locality. At Sawady in the Tengleng Stream, also at Bhamo and at Shuaygoomyo.

(3) Topotypes Examined. Myanmar: Nam Sa Yi River near Bhamo, 24.2196° N, 97.2224° E, Ayeyarwady Basin, 30.xi.2016, 10 specimens (RMBH biv 262, including biv 262/1, biv 262/2 and biv 262/4 (MNCN 15.07/14235) sequenced), Vikhrev and Nyein Chan leg.; Nam Pha Lake near Bhamo, 24.2972° N, 97.2610° E, Ayeyarwady Basin, 29.xi.2016, 12 specimens (RMBH biv 257, including biv 257/1, biv 257/6 and biv 257/9 sequenced), Vikhrev and Nyein Chan leg.; Shwe Kyi lake near Bhamo, 24.2927° N, 97.2299° E, Ayeyarwady Basin, 29.xi.2016, 10 specimens (RMBH biv 261, including biv 261/3, 261/6 and 261/7 sequenced), Vikhrev and Nyein Chan leg.; Myaung lake near Bhamo, 24.2387° N, 97.1658° E, Ayeyarwady Basin, 01.xii.2016, 10 specimens (RMBH biv 264, including biv 264/1, biv 264/4 and biv 264/7 sequenced), Vikhrev and Nyein Chan leg. (Figure 5(a)).

(4) Tapparone-Canefri's Type Material and Recent Topotypes Examined. *Unio marginalis* var. *subflabellata* Tapparone-Canefri, 1889: Holotype (by original designation) in MSNG labelled "*Unio marginalis*, Lk. var. *subflabellata*, Tapp. Can., Ann. M. C. Gen. XXVII, 1889, p. 346 (Tipo della varieta!). Mandalay, del mercato, Dic(embre). 1885 – Genn(aio). 1886. Leg. L. Fea!". Type locality: Mandalay, del mercato (Mandalay market). Topotype material examined: ox-bow lake near Ta Naung Taig village, 21.4064° N, 95.3399° E, Ayeyarwady Basin, 03.iii.2018, 3 specimens (RMBH biv 427A, including biv 427A/1 and biv 427A/2 sequenced), Bolotov, Vikhrev, and Nyein Chan leg. (Figures 5(e), 5(g), 5(h)).

(5) Tapparone-Canefri's Non-Type Material and Recent Sample Examined. One shell in MSNG labelled "*Unio marginalis* Lk. var. *tricolor* Hanl. & Theob. - Tapp. Ann. M. C. Gen. XXVII, 1889, p. 347. Mandalay, del mercato. Dic(embre). 1885 – Genn(aio). 1886. L. Fea!". Recent material from this locality: Ayeyarwady River at Mandalay city, 21.9909° N, 96.0610° E, 04.iii.2018, 1 specimen (RMBH biv 442/3 sequenced), Bolotov, Nyein Chan, and Vikhrev leg. (Figures 5(d), 5(f)).

(6) Other Material Examined. Myanmar: Pathi River, 19.0278°N, 96.5353°E, Sittaung Basin, 23.xi.2016, 2 specimens (RMBH biv 242/8 and biv 242/15 sequenced), Vikhrev and Nyein Chan leg.; Nadi Lake, 20.6858°N, 96.9316°E, Salween Basin, 23.02.2018, 11 specimens (RMBH biv 399, including biv 399/1 and biv 399/2 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Hnit Saung Pyang Stream, 19.5140°N, 96.2621°E, Sittaung Basin, 28.ii.2018, 1 specimen (RMBH biv 408 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Sin Thay Dam, 20.1540°N, 96.1149°E, Sittaung Basin, 01.iii.2018, 10 specimen (RMBH biv 413, including biv 413/1, biv 413/2 and biv 413/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Mone Ding Dam outlet, 20.8099°N, 95.7242°E, Ayeyarwady Basin, 01.iii.2018, 7 specimens (RMBH biv 415 and biv 416, including biv 415/1, biv 415/2, biv 415/3, biv 416/1, biv 416/2, and biv 416/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Sin Khong Stream, 22.0632°N, 96.0810°E, Ayeyarwady Basin, 04.iii.2018, 3 specimens (RMBH biv 439), Bolotov, Vikhrev, and Nyein Chan leg.

(7) Distribution. Ayeyarwady, Salween, and Sittaung basins.

(8) Comments. In the Ayeyarwady Basin, this species appears to have a rather restricted range and is confined to the middle part of this freshwater system.

4.6. Genus Trapezidens Bolotov, Vikhrev & Konopleva, 2017 (Subfamily Parreysiinae Henderson, 1935, Tribe Lamellidentini Modell, 1942). Type species: *Unio exolescens* Gould, 1843 (by original designation).

4.6.1. Trapezidens dolichorhynchus (Tapparone-Canefri, 1889). =Unio dolichorhynchus Tapparone Canefri, 1889: 348 [15] (Figure 5(l)).

=*Unio protensus* var. *ellipticus* Tapparone-Canefri, 1889: 350 [15] (Figure 5(k)).

=*Unio gianellii* Tapparone-Canefri, 1889: 353 [15] (Figure 5(j)).

=*Unio gianelli* var. *degener* Tapparone-Canefri, 1889: 354 [15] (new junior synonym).

=*Unio protensus* Tapparone-Canefri, 1889: 349 [15] (Figure 5(i)).

=*Unio marginalis* Tapparone-Canefri, 1889: 345 [15] (Figure 5(m)).

=*Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889). – Bolotov et al., 2018: 3 [18]; Konopleva et al., 2020: 52 [30].

Figures 5(i)–5(m), 7, and 8, Tables 2 and 3, Figures S1 and S4.

(1) Type. Whereabouts unknown.

(2) Type Locality. Mercato di Mandalay (L. Fea) (Ayeyarwady River at Mandalay city (bought in a city market), approx. 21.9491°N, 96.0483°E, Myanmar).

(3) Topotypes Examined. Myanmar: Ayeyarwady River at Mandalay city, 21.9909° N, 96.0610° E, 04.iii.2018, 2 specimens (RMBH biv 442/1 and biv 442/2 sequenced), Bolotov, Nyein Chan, and Vikhrev leg

(4) Tapparone-Canefri's Material Examined. The specimens were not located in the MSNG

(5) Other Material Examined. Myanmar: Ayeyarwady River near Tant Kyi village, 21.1567°N, 94.8050°E, 02.iii.2018, 16 specimens (RMBH biv 417, including specimens biv 417/1, biv 417/2, and biv 417/3 sequenced), Bolotov, Nyein Chan, and Vikhrev leg.; Ayeyarwady River at Thin Baw Kone village, 21.3145°N, 95.05889°E, 02.iii.2018, 1 specimen (RMBH biv 423, only shell), Bolotov, Nyein Chan, and Vikhrev leg.; Myit Tha (Manipur) River, 23.22845°N, 94.1434°E, Ayeyarwady Basin, 02.ii.2018, 6 specimens (RMBH biv 336, including biv 336/1, biv 336/2, and biv 336/3 sequenced), Bolotov, Nyein Chan, and Vikhrev leg; Chindwin River, 23.1499°N, 94.3627°E, Ayeyarwady Basin, 04.ii.2018, 7 specimens (RMBH biv 353 and biv 354, including biv 353, biv 354/1, biv 354/2, and biv 354/3 sequenced), Bolotov, Nyein Chan, and Vikhrev leg.

(6) Distribution. Endemic to Myanmar: widespread throughout the Ayeyarwady Basin.

(7) Comments. Here, we present an updated synonymy of this species.

4.7. Genus Yaukthwa Konopleva et al., 2019 (Subfamily Gonideinae Ortmann, 1916, Tribe Contradentini Modell, 1942). Type species: *Trapezoideus nesemanni* Konopleva, Vikhrev & Bolotov, 2017 (by original designation).

4.7.1. Yaukthwa nesemanni (Konopleva, Bolotov & Kondakov, 2017). =*Unio sella* Prashad, 1922: 93 [16] (unavailable name: introduced as a synonym of *Unio laosensis* Lea, 1863) [28].

=*Margaritanopsis laosensis* Prashad, 1922: 93 [16] (identification error) [28].

=*Trapezoideus nesemanni* Konopleva, Bolotov & Kondakov, 2017. – Bolotov et al., 2017: 13 [24].

=*Yaukthwa nesemanni* (Konopleva, Bolotov & Kondakov, 2017). – Konopleva et al., 2019: 7 [20].

Figures 6(a)–6(c), and 8, Tables 2 and 3, Figure S5.

(1) Type. Holotype NCSM 103033 (transferred from RMBH biv255/2) labelled "Myanmar: Sittaung, Tauk Ue Kupt River, 26.xi.2016, Vikhrev and Nyein Chan leg." (NCSM).

(2) Type Locality. Tauk Ue Kupt River, Sittaung Basin, Myanmar [24].

(3) Type Material Examined. The type series of *Yaukthwa nesemanni* (RMBH biv 144/14, biv 144/19, biv 144/25 and biv 255/3).

(4) Tapparone-Canefri's Material Examined. One shell in MSNG labelled "*Unio sella* Tapp. n. sp. (in lit.). Carin independ. 1000-1200 m".

(5) Other Material Examined. Myanmar: the same locality as for the type, NCSM 103031 (transferred from RMBH biv 144/7 and biv 144/17) and RMBH biv 144 and biv 255, Bolotov, Vikhrev, and Nyein Chan leg.; Chindwin River, 23.1499°N, 94.3629°E, Ayeyarwady Basin, 04.ii.2018, 1 specimen (RMBH biv 351 sequenced), Bolotov, Nyein Chan, and Vikhrev leg.; Cho River, 19.5069°N, 96.5618°E, Sittaung Basin, 2.ii.2018, 10 specimens (RMBH biv 405, including biv 405/1 and biv 405/3 sequenced), Bolotov, Nyein Chan, and Vikhrev leg.; Ayeyarwady River at Mandalay, 21.9574°N, 96.0510°E, 03.iii.2018, 1 specimen (RMBH biv 437 sequenced), Bolotov, Nyein Chan, and Vikhrev leg.; Nant Poat Kalay River, 24.2130°N, 96.1089°E, Ayeyarwady Basin, 13.xi.2018, 12 specimens (RMBH biv 607, biv 608 and biv 609, including biv 607/1, biv 607/2, biv 607/3, biv 608/1, biv 608/2 and biv 608/3 sequenced), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg.; Indaw River near Sell Ywar village, 24.2123°N, 96.0819°E, Ayeyarwady River basin, 14.xi.2018, 15 specimens (RMBH biv 612 and biv 613 (only 5 tissue snips), including biv 612/1, biv 612/2, biv 612/3, biv 613/1, biv 613/2 and biv 613/3 sequenced), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg.; Myanmar: Haungthayaw River near Mi Kwee village, 15.962°N, 98.41522°E, 16.ii.2020, 1 specimen (RMBH biv 1022/3 sequenced), Than Win leg.

(6) Distribution. Sittaung, Ayeyarwady, and Haungthayaw Basins.

(7) Comments. Leonardo Fea collected this sample during his travel throughout the Karin Hills, a highland area with rapidly flowing mountain rivers and

streams [28]. Fea's sample from MSNG was described and illustrated in detail [28].

4.7.2. Yaukthwa rectangularis (Tapparone-Canefri, 1889). =*Unio rectangularis* Tapparone-Canefri (1889): 354 [15].

=*Margaritanopsis rectangularis* (Tapparone-Canefri, 1889). – Prashad, 1922: 93 [16].

=*Trapezoideus subclathratus* Bolotov et al., 2017: 10 [24] (identification error).

=*Yaukthwa dalliana* Bolotov et al., 2019: Supplementary Table 1 [23] (identification error).

=*Yaukthwa dalliana* Konopleva et al., 2019: 7 [20] (identification error).

=*Indonaia rectangularis* (Tapparone-Canefri, 1889). – Bolotov et al., 2019: 25 [27].

=*Yaukthwa rectangularis* (Tapparone-Canefri, 1889). – Pfeiffer et al., 2021: 437 [22] (new combination).

Figures 6(d), 6(e), and 8, Tables 2 and 3, Fugure S5.

(1) Type. Holotype (by monotypy) labelled "*Unio rectangularis* Tapp. Can. Teinzo, Mti E. di Bhamo (L. Fea)" (MSNG; examined by us).

(2) Type Locality. Teinzo, nel fiume Mule, Monti E. di Bhamo (Mole Stream (Mole Chaung in Burmese) near Teinthaw village, 24.3978°N, 97.2519°E, Ayeyarwady Basin, Myanmar) [15].

(3) Topotypes Examined. Myanmar: Mole Stream, 24.4010°N, 97.2544°E, Ayeyarwady River basin, 11.iii.2020, 7 specimens (RMBH biv 916, including biv 916/1, biv 916/2 and biv 916/3 sequenced; RMBH biv 917/1 sequenced), Nyein Chan leg.

(4) Other Material Examined. Myanmar: Pan Khai Stream, 27.4493°N, 97.3432°E, Mali Hka River, Ayeyarwady Basin, 13.iii.2014, 10 specimens (RMBH biv 101, including biv 101/4, biv 101/5 and biv 101/6 sequenced), Bolotov and Vikhrev leg.; Nam Balak River, 27.4741°N, 97.3493°E, Mali Hka River, Ayeyarwady Basin, 13.iii.2014, 10 specimens (RMBH biv 102, including biv 102/7, biv 102/11 and biv 102/14 sequenced), Bolotov and Vikhrev leg.; Mansakun River, 27.4909°N, 97.3351°E, Mali Hka River, Ayeyarwady Basin, 13.iii.2014, 5 specimens (RMBH biv 103, including biv 103/17, biv 103/18 and biv 103/19 sequenced), Bolotov and Vikhrev leg.; unnamed stream, 27.5475°N, 97.3705°E, Mali Hka River, Ayeyarwady Basin, 14.iii.2014, 3 specimens (RMBH biv 104, including biv 104/34 and biv 104/35 sequenced), Bolotov and Vikhrev leg.; Nam Shu River, 27.5482°N, 97.3700°E, Mali Hka River, Ayeyarwady Basin, 14.iii.2014, 14 specimens (RMBH 105, including biv 105/24, biv 105/31 and biv 105/32 sequenced), Bolotov and Vikhrev leg.; Nanuinhka Chaung River, 25.0815°N, 96.2874°E, Ayeyarwady Basin, 25.iii.2014, 37 specimens (RMBH biv 111, including biv 111/2, biv 111/21 and biv 111/43 sequenced), Bolotov and Vikhrev leg.; Indaw River, 25.5274°N, 96.7189°E, Ayeyarwady Basin, 13.iii.2020, 10 specimens (RMBH biv 937, including biv 937/1, biv 937/2 and biv 937/3 sequenced), Bolotov, Nyein Chan, Vikhrev, Kondakov, and Gofarov leg.; Mogaung River, 25.3151°N, 96.9326°E, Ayeyarwady Basin, 14.iii.2020, 4 specimens (RMBH biv 961, including biv 961/1, biv 961/2 and biv 961/3 sequenced), Bolotov, Nyein Chan, Vikhrev, Kondakov, and Gofarov leg.; Mogaung River, 25.3151°N, 96.9326°E, Ayeyarwady Basin, 14.iii.2020, 11 specimens (RMBH biv 964, including biv 964/1, biv 964/2 and biv 964/3 sequenced), Bolotov, Nyein Chan, Vikhrev, Kondakov, and Gofarov leg.; Nantyin Stream, 25.02712°N, 96.6183°E, Ayeyarwady Basin, 14.iii.2020, 23 specimens (RMBH biv 974 and biv 976, including biv 974/1, biv 974/2, biv 974/3, biv 976/1, biv 976/2 and biv 976/3 sequenced), Bolotov, Nyein Chan, Vikhrev, Kondakov, and Gofarov leg.

(5) Distribution. This species inhabits mountain rivers and streams belonging to the Upper Ayeyarwady Basin.

(6) Comments. Bolotov et al. [27] re-described and illustrated this species in detail. It was transferred to the genus *Indonaia* Prashad, 1918 based on conchological features. Later, Pfeiffer et al. [22] argued that this species belongs to the Contradentini, and, more specifically, is a member of the genus *Yaukthwa*. This morphology-based taxonomic hypothesis was supported by our new DNA sequences of topotypes from the Mole Stream. Furthermore, a *Yaukthwa* species from mountain rivers and streams of the Upper Ayeyarwady Basin identified to be conchologically similar to *Y. dalliana* (see [20, 23]) is in fact *Y. rectangularis*. Furthermore, sequenced topotypes of *Yaukthwa dalliana* revealed that it is a valid species having a restricted range in a section of the Lashio River near the town of Lashio (Figures 6(f) and 6(g)).

4.7.3. Yaukthwa zayleymanensis (Preston, 1912). =*Unio foliaceus* Tapparone-Canefri, 1889: 345 [15] (identification error).

=*Trapezoideus foliaceus* var. *zayleymanensis* Preston, 1912: 307 [50].

=*Yaukthwa zayleymanensis* (Preston, 1912). – Konopleva et al., 2019: 8 [20].

Figures 6(h)–6(k), and 8, Tables 2 and 3, Figure S5.

(1) Type. Syntype SMF 3615 (Figure 6(h)).

(2) Type locality. Bhamo (Bhamo, Ayeyarwady River, Myanmar) and Zayleyman (a locality in the Ayeyarwady Basin, Myanmar) [50].

(3) Topotypes Examined. Myanmar: Tarkat Stream, 25.2758°N, 97.2722°E, Ayeyarwady Basin, 23.iii.2018, 5 specimens (RMBH biv 679, including biv 679/1, biv 679/2 and biv 679/3 sequenced), Nyein Chan leg. (Figure 6(i)).

(4) Tapparone-Canefri's Material Examined. One shell in MSNG labelled "*Unio foliaceus* Gould var. *fragilis*

Nev. A. Birmania: Teinzo. L. Fea!" (Mole Stream near Teinthaw village, 24.3978°N, 97.2519°E, Ayeyarwady Basin, Myanmar) (Figures 6(j) and 6(k)).

(5) Other Material Examined. Myanmar: Ayeyarwady River, 21.8893°N, 95.9978°E, Mandalay, 04.iii.2018, 2 specimens (RMBH biv 448, including biv 448/1 and biv 448/2 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Bani River, 19.3247°N, 94.9839°E, Ayeyarwady Basin, 09.xii.2018, 11 specimens (RMBH biv 665, including biv 665/1 and 665/3 sequenced; RMBH biv 666/6 sequenced), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg.; Lamon Chaung Stream, 26.3463°N, 96.66855°E, Ayeyarwady Basin, January 2020, 2 specimens (RMBH biv 899, all sequenced), local collectors leg.; Mole Stream, 24.4010°N, 97.2544°E, Ayeyarwady Basin, 11.iii.2020, 12 specimens (RMBH biv 917/2 and biv 917/3 sequenced; RMBH biv 918, including biv 918/1, biv 918/2 and biv 918/3 sequenced), Nyein Chan leg.; Mogaung River, 25.3151°N, 96.9326°E, Ayeyarwady Basin, 14.iii.2020, 9 specimens (RMBH biv 963, including biv 963/1, biv 963/2 and biv 963/3 sequenced), Bolotov, Vikhrev, Nyein Chan, Kondakov, and Gofarov leg

(6) Distribution. Ayeyarwady River basin.

(7) Comments. Although a reliable identification of *Yaukthwa* taxa using conchological features alone is complicated, Tapparone-Canefri's specimen from the Mole Stream clearly corresponds to *Yaukthwa zayleymanensis* conchologically. This genus contains a number of local endemic species, the range of which is restricted by a certain freshwater basin or even to a tributary of a river or a lake [20]. Our new sequenced sample from the Mole Stream was similar to the Tapparone-Canefri's specimen based on morphological features, and was found to belong to *Yaukthwa zayleymanensis*.

4.8. Genus Trapezoideus Simpson, 1900 (Subfamily Gonideinae Ortmann, 1916, Tribe Contradentini Modell, 1942). Type species: *Unio foliaceus* Gould, 1843 (by original designation).

4.8.1. Trapezoideus mitanensis Bolotov, Konopleva, Than Win, Kondakov & Vikhrev Sp. Nov. =Unio exsolescens (sic) Tapparone-Canefri, 1889: 345 [15] (identification error and incorrect spelling of *Unio exolescens* Gould, 1843; sampling locality: Meetan, fiume Houngdarau (Mitan Stream, 15.9999°N, 98.3946°E, a tributary of the upstream section of the Haungthayaw River, Myanmar); this sample was not located in MSNG).

=*Trapezoideus exolescens* Prashad, 1922: 109 [16] (partim; identification error).

Figures 6(l)–6(n), and 8, Tables 2 and 3, Figure S5.

(1) LSID. http://zoobank.org/urn:lsid:zoobank.org:act:EA9B9305-E615-403B-B9D5-7488507D0196

(2) Holotype. RMBH biv 1021/1: Myanmar: Mitan Stream near Mitan village, 16.0017°N, 98.4064°E, Haungthayaw River basin, 16.ii.2020, Than Win leg. Reference sequence number of the holotype is as follows: OL597613 (*COI*), ON142670 (*16S rRNA*) and ON171238 (*28S rRNA*). Shell measurements of the holotype are as follows: shell length (SL) =37.1 mm, shell height (SH) =20.8 mm, and shell width (SW) =12.3 mm (Table S4).

(3) Paratypes. The same locality, date, and collector, 9 specimens (RMBH biv 1021, including biv 1021/2 and biv 1021/3 sequenced); Myanmar: Haungthayaw River near Mi Kwee village, 15.9620°N, 98.4152°E, 16.ii.2020, 2 specimens (RMBH biv 1022/1 and biv 1022/2 sequenced), Than Win leg.

(4) Etymology. This species is named after its type locality, the Mitan Stream, a tributary of the Haungthayaw River in Myanmar.

(5) Differential Diagnosis. The new species has a number of conchological traits typical for the genus *Trapezoideus* such as a trapezoidal shell shape, small umbo, thin and lamellar teeth, and shallow muscle scars. Young specimens are broader posteriorly, with a higher dorsal margin, while adults are more elongated and more similar to *Yaukthwa* representatives.

(6) Molecular Diagnosis. The new species differs from other *Trapezoideus* taxa by the fixed nucleotide substitutions: 16 substitutions in the *COI* gene fragment (8 G, 68 A, 71 T, 107 C, 149 G, 182 G, 194 C, 200 A, 230 A, 266 A, 272 A, 311 A, 323 A, 429 C, 579 C, 593 C), 9 substitutions in the *16S rRNA* gene fragment (195 G, 234 A, 236 G, 248 G, 249 T, 269 T, 297 A, 319 C, 336 C), and a substitution in the nuclear *28S rRNA* gene (620 C).

(7) Description. Shell small, trapezoidal, thin, moderately inflated, rounded anderiorly, broad and truncated posteriorly, dorsal margin slightly high, ventral margin usually straight. Umbo small, elevated above hinge line, eroded, young specimens seem to have a sculptured umbo with somewhat nodulose wrinlkes. Area from umbo along dorsal margin covered by fine wrincles. Periostracum of young specimens yellow olive, posterior margin can be covered with pale green stripes. Periostracum of adults usually brown, posterior and ventral margins can be partly rusty colored. Shell surface with dense growth lines. Nacre bluish. Pseudocardinal teeth slender, two on right valve and one on left valve, reduced for some specimens. Lateral teeth thin, slightly curved, one on right valve and two on left valve. Muscle attachement scars very shallow or reduced.

(8) Distribution. Haungthayaw River basin.

(9) Comments. Based on the morphological description and distribution [15], we assumed that this freshwater mussel can be an undescribed *Yaukthwa* species.

Conversely, new samples collected from the Mitan Stream and the main channel of the Haungthayaw River revealed that it is a new species of the genus *Trapezoideus*.

4.9. Genus Pseudodon Gould, 1844 (Subfamily Gonideinae Ortmann, 1916, Tribe Pseudodontini Frierson, 1927). Type species: *Anodon inoscularis* Gould, 1844 (by original designation).

4.9.1. Pseudodon kayinensis Bolotov et al., 2020. =Pseudodon inoscularis Tapparone-Canefri, 1889: 355 [15] (identification error).

=*Pseudodon kayinensis* Bolotov et al., 2020: 14 [17].

Figures 6(o), 6(p), and 8, Tables 2 and 3.

(1) Type. Holotype RMBH biv 618/1.

(2) Type Locality. Myanmar: Winyaw River, 15.6685°N, 97.9496°E, Ataran River basin.

(3) Material Examined. The type series of *Pseudodon kayinensis*; Myanmar: Donthami Maw Stream near Lel Taw Gyi village, 16.0026°N, 98.3796°E, Haungthayaw Basin, 16.ii.2020, 2 specimens (RMBH biv 1026, including biv 1026/1, biv 1026/2 and biv 1026/3 sequenced), Than Win leg.; unnamed stream near Naung Ta Kho village, 16.0674°N, 98.2946°E, Haungthayaw Basin, 16.ii.2020, 2 specimens (RMBH biv 1026A), Than Win leg.

(4) Distribution. Ataran, Hlaingbwe, and Haungthayaw basins.

(5) Comments. The status and distribution of the nominal taxon *Pseudodon inoscularis* are unclear. John Pfeiffer (pers. comm. 2020) assumed that *Pseudodon inoscularis* inhabits the Moei Basin, a tributary of the Salween River flowing north along the border between Myanmar and Thailand. However, there is some evidence that the lectotype of *Pseudodon inoscularis* was collected by Rev. F. Mason from the Dawei (Tavoy) River (our unpublished data). This taxonomic puzzle needs further research efforts.

5. Discussion

5.1. Taxonomic Summary. Our results show that the proportion of correct identifications of freshwater mussel taxa in historical works such as that of Tapparone-Canefri [15] could even be lower than it was previously suggested (e.g., [16]). This evidence indicates that preparing checklists of freshwater mussel species by means of a direct compilation of historical data (e.g., [31, 57]) may lead to unreliable species richness estimates biased by multiple identification errors. In summary, collection of freshwater mussels from British Burma examined and published by Tapparone-Canefri [15] contains 13 taxa that were listed as 34 nominal species (Table 2). The valid taxa in those samples are as follows: *Indochinella pugio pugio*, *I. pugio paradoxa*, *Indonaia andersoniana*, *Lamellidens generosus*, *L. savadiensis*, *Leoparreysia tavoyensis*, *Pseudodon kayinensis*, *Radiatula chaudhurii*, *R. mouhoti haungthayawensis*, *Trapezidens dolichorhynchus*, *Yaukthwa zayleymanensis*, *Y. rectangularis*, and *Trapezoideus mitanensis* sp. nov. A relatively low species richness in Leonardo Fea's collection can be explained by a small number of sampling localities mostly situated within two river basins, i.e. the Ayeyarwady and Haungthayaw (Table 1). Additionally, Tapparone-Canefri identified samples of *Gibbosula laosensis* and *Yaukthwa nesemanni* from a tributary of the Sittaung River as *Unio sella*, although this name has never been introduced as such but was repeatedly published as a synonym [28]. Currently, only two species are considered valid among the new taxa described by Tapparoni-Canefri [15], i.e. *Trapezidens dolichorhynchus* and *Yaukthwa rectangularis* (Table 2).

Trapezoideus mitanensis sp. nov. from the Haungthayaw River represents a fourth species in this small genus belonging to the tribe Contradentini [17, 22]. This lineage has a high level of genetic divergence from its congeners, sharing diagnostic substititions in all the studied gene fragments.

5.2. Conchological Variability and Synonymy of Leoparreysia tavoyensis. Among the studied taxa, *Leoparreysia tavoyensis* was found to be the most conchologically variable species. Six nominal species such as *Unio luteus*, *U. bhamoensis*, *U. mandelayensis*, *U. feae*, *U. houngdarauicus*, and *Parreysia choprae* are synonymized here with *L. tavoyensis* based on the study of topotypes by means of morphological, molecular, and phylogenetic analyses. Each of these morpho-species differs from others by having a more or less specific shell shape, sculpture, color and surface of periostracum or even structure of the teeth (Figure 3). Until today these taxa were not subjected by detailed taxonomic revision. *Unio luteus* was synonymised with *Parreysia corrugata* by Simpson [58] and since then its taxonomic position has not been changed by other malacologists [54, 57, 59–61]. While revising the Tapparone-Canefri's [15] work, Prashad [16] recognized *Unio bhamoensis*, *U. mandelayensis*, *U. feae*, and *U. houngdarauicus* as separate species belonging to the genus *Parreysia*. Later Prashad [53] described the new species *Parreysia choprae* from Indawgyi Lake which till now had a status of valid species but within the genus *Leoparreysia* [24, 26]. Haas [60] synonymized *Unio mandelayensis* and *U. bhamoensis* leaving only one valid species *Parreysia bhamoensis.* According to the range of subsequent works, this taxon was transferred to the genus *Leoparreysia* [21, 24, 26, 62]. In return, *Unio feae* and *U. houngdarauicus* until recently had saved their status of separate taxa [24, 26]. Though Haas [60] synonymized *Unio houngdarauicus* with *Parreysia tavoyensis*, *P. feae* from the same river basin was considered a valid species. Regarding *Unio parma* Sowerby, 1868, this taxon was transferred to *P. tavoyensis* by Prashad [16] and Haas [60]. However, the subsequent revisions were not conducted.

This fact that so many researchers recognised the validity of taxa, discussed above, confirmed the high conchological variability of *Leoparreysia tavoyensis* and difficulty in distinguishing it using morphological methods alone. This variable species is widespread throughout Myanmar, and it was recorded in almost all large and medium-sized river

basins of the country. It is clear that a large amount of intraspecific conchological forms in *Leoparreysia tavoyensis* may reflect environmental gradients such as habitat (rivers, streams or lakes) and substrate type.

5.3. Historical Market Trade of Freshwater Mussels in the Former British Burma. Another interesting issue of this study is that the samples of several species, i.e. *Indonaia andersoniana*, *Indochinella pugio pugio*, and *Lamellidens generosus*, were obtained by Leonardo Fea from a market (del mercato) in the city of Mandalay [15]. This evidence indicates that freshwater mussels were historically used in the market trade in Myanmar at least since the 1880s. One might think that the most appropriate usage of these mussels was for consumption, as food and cooking. However, it is strange that the contemporaries of that historical period, e.g. F. Mason and W. Theobald in their work ([63]: p. 129-131), did not mention that the Unionidae were used for eating in Burma as opposed to marine and estuarine bivalves.

Currently, freshwater bivalves are actively harvested for food and market trade throughout Southeast and South Asian countries, i.e. Myanmar, Laos, Vietnam, Indonesia, and India [18, 57, 64–66]. A range of species is used for local sale, production of decorative, art goods, and jewellery, as well as producing artificial freshwater pearls [67]. Allen et al. [68] noted that freshwater biological resources such as molluscs play a vital role in the everyday life of local communities. We could assume that freshwater mussels in the local markets in the former British Burma were used with similar purposes and were actively involved in trading.

Nowadays an international export of freshwater mussels for aquaria is also widespread. According to the recent work of Ng et al. [69], several freshwater mussel species endemic to Myanmar such as *Leoparreysia olivacea* and *L. tavoyensis* were recorded among molluscs involved in ornamental pet trade in Singapore during the period of 2008 to 2014.

Harvesting and over-exploitation are one of the biggest threats to freshwater mussel populations throughout Southeast Asia, especially to local endemic and rare species [65, 67]. Our present study is one more part of the research helping to understand unionoid systematics in Myanmar and the Oriental tropics generally and to create a scientific basis for environmental management and conservation planning.

Data Availability

The morphometric, sequence, molecular and phylogenetic data used to support the findings of this study are included within the supplementary information files.

Conflicts of Interest

The authors declare no conflict of interest.

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Supplementary Materials

Figure S1. Shell proportions of *Lamellidens* and *Trapezidens* based on the shell elongation index (SEI). The bold lines show a 95% confidence ellipses. Figure S2. Maximum likelihood phylogeny of the mitochondrial data set (three codons of *COI*) of the Indochinellini from Myanmar. Scale bar indicates the branch lengths. Black numbers near nodes are ML ultrafast bootstrap support values (BS)/Bayesian Posterior Probabilities (BPP). River basins are shown by different colors. Outgroup (*Gibbosula laosensis, Margaritifera dahurica*, *Parreysia rakhinensis*, *Leoparreysia olivacea*, and *L. tavoyensis*) is not shown. Figure S3. Maximum likelihood phylogeny of the mitochondrial data set (three codons of *COI*) of the Leoparreysiini from Myanmar. Scale bar indicates the branch lengths. Black numbers near nodes are ML ultrafast bootstrap support values (BS)/Bayesian Posterior Probabilities (BPP). River basins are shown by different colors. Outgroup (*Gibbosula laosensis, Margaritifera dahurica*, and *Parreysia rakhinensis*) is not shown. Figure S4. Bayesian phylogeny of the mitochondrial data set (three codons of *COI*) of the Lamellidentini from Myanmar. Scale bar indicates the branch lengths. Black numbers near nodes are Bayesian Posterior Probabilities (BPP)/ML ultrafast bootstrap support values (BS). River basins are shown by different colors. Outgroup (*Gonidea angulata*, *Leguminaia wheatleyi, Potomida littoralis*, and *Lamprotula leai*) is not shown. Figure S5. Bayesian phylogeny of the mitochondrial data set (three codons of *COI*) of the Contradentini from Myanmar. Scale bar indicates the branch lengths. Black

numbers near nodes are Bayesian Posterior Probabilities (BPP)/ML ultrafast bootstrap support values (BS). River basins are shown by different colors. Outgroup (*Gonidea angulata*, *Leguminaia wheatleyi, Potomida littoralis*, and *Lamprotula leai*) and the haplotypes of the genus *Lens* are not shown. Table S1. List of sequences of the Unionidae from Southeast Asia used in this study. Table S2. The best-fit models of nucleotide substitution and partition scheme. Table S3. Genetic divergences (mean uncorrected p-distances, %) from *Trapezoideus mitanensis* sp. nov. and its congeners based on the mitochondrial *COI* gene sequences. Table S4. Shell parameters (mm) and reference DNA sequences for the type series of *Trapezoideus mitanensis* sp. nov. from Myanmar. Alignment S1. 3 codons of *COI*+16*S rRNA*+28*S rRNA* sequence alignment. Alignment S2. *COI* sequence alignment of Indochinellini from Myanmar. Alignment S3. *COI* sequence alignment of Leoparreysiini from Myanmar. Alignment S4. *COI* sequence alignment of Lamellidentini from Myanmar. Alignment S5. *COI* sequence alignment of Contradentini from Myanmar. *(Supplementary Materials)*

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