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

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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*, *Raditula chauhdhuri*, *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 synonyms for several conchologically variable species such as Leoparreysia tavoyensis (Gould, 1843), Trapezidens dolichorhynchus (Tapparone-Canefri, 1889), Lamellidens generous (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 conchological analyses were carried out applying differences of the shell shape, hinge plate, umbo position, muscle attachment scars,
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. *subflabelata* 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 described 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).

<table>
<thead>
<tr>
<th>Code</th>
<th>Original label(s)</th>
<th>Locality data</th>
<th>Approximate geographic coordinates</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>HG-01</td>
<td>Tenasserim: Meetan, fiume Hougndara</td>
<td>Mitau stream (Mitau Chaung in Burmese), a tributary of the upstream section of the Haungthayaw River, Myanmar</td>
<td>Latitude: 15.9999 Longitude: 98.3946</td>
<td>Tapparone-Canefri [15]</td>
</tr>
<tr>
<td>HG-03</td>
<td>Mandalay; mercato di Mandalay</td>
<td>Ayeyarwady River and/or floodplain lakes at Mandalay city (bought in a city market), Myanmar</td>
<td>Latitude: 21.9491 Longitude: 96.0483</td>
<td>Tapparone-Canefri [15]</td>
</tr>
<tr>
<td>HG-05</td>
<td>Teinzo del mule Chaung; Teinzo, N. E. di Bhamò; Teinzo, nel fiume mule, Monti E. di Bhamò; A(lta). Birmania: Teinzo</td>
<td>Mole stream (mole Chaung in Burmese) at Teintha village, Ayeyarwady Basin, Myanmar</td>
<td>Latitude: 24.3978 Longitude: 97.2519</td>
<td>Tapparone-Canefri [15]; Bolotov et al. [27]</td>
</tr>
<tr>
<td>ST-01</td>
<td>Carin independ. 1000-1200 m</td>
<td>Upstream section of the Taok Ue Kupt River, Sittaung Basin, Myanmar</td>
<td>Latitude: 19.3075 Longitude: 96.7219</td>
<td>Bolotov et al. [28]</td>
</tr>
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</table>

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, Radianula chaudhuri and R. mouhoti haungthyawensis (Figure 2), Leoparreysia tavoyensis (Figure 3), Lamellidens generous (Figure 4), L. savadiensis and Trazepidens dolichorhynchos (Figure 5), Yaukthwa nesmanni 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. marginals var. sublabellata (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>
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<th>Page</th>
<th>Nominal taxon by Tapparone-Canefri (1889 and collection labels) (original spelling and authorship)</th>
<th>Re-identification by Prashad (1922) (original spelling and authorship)</th>
<th>Label data [old locality code; See Table 1 for detail]</th>
<th>Modern taxonomic placement</th>
<th>Tapparone-Canefri’s sample depository</th>
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<td>Pseudodon inoscularis Gould</td>
<td><em>Pseudodon vondembuschiana</em> var. <em>inoscularis</em> (Gould)</td>
<td>Meetan, fiume Houngdarau (L. Fea) [HG-01]</td>
<td><em>Pseudodon kayinensis</em> Bolotov et al., 2020</td>
<td>Whereabouts unknown (probably in ZSI)</td>
<td>Only specimens of <em>Pseudodon kayinensis</em> 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))</td>
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<td>343</td>
<td>Unio bonneaudii Eydoux et Souleyet, 1838</td>
<td><em>Indonaia bonneaudi</em> (Eydoux)</td>
<td>Meetan, fiume Houngdarau (L. Fea) [HG-01]</td>
<td><em>Radiatula mouhoti</em> haungthayawensis Bolotov et al., 2019</td>
<td>Whereabouts unknown</td>
<td>Based on the description, distribution, and molecular data on the type series of <em>Radiatula mouhoti</em> haungthayawensis (see [23]) (Figure 2(q))</td>
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<td>343, 344</td>
<td>Unio burmanus Blanford, 1869</td>
<td>N/A</td>
<td>Label: Teinzo del mule Chaung – Marz. 1886. L. Fea. Published label data: Teinzò, nel fiume mule, N. E. di Bhamò [AY-03]</td>
<td><em>Radiatula chaudhurii</em> (Preston, 1912)</td>
<td>MSNG</td>
<td>Tapparone-Canefri’s sample examined; new samples from the locality sequenced (this study) (Figures 2(n)–2(p))</td>
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<td>Unio coerules Lea, 1852</td>
<td><em>Indonaia caerulea</em> (Lea)</td>
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<td><em>Indonaia andersoniana</em> (Nevill, 1877)</td>
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<td>Tapparone-Canefri’s sample examined; new samples from the locality sequenced (this study) (Figures 2(d)-2(f), and 2(h))</td>
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<td>Unio corrianus Lea</td>
<td><em>Lamellidens corrianus</em> (Lea)</td>
<td>Mandalay, del mercato [AY-01]</td>
<td><em>Lamellidens generosus</em> Gould, 1847</td>
<td>MSNG</td>
<td>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))</td>
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<td>Unio crispatus Gould</td>
<td><em>Indonaia crispata</em> (Gould)</td>
<td>Meetan, fiume Houngdarau (L. Fea) [HG-01]</td>
<td><em>Indochinella pugio paradoxa</em> Bolotov et al., 2019</td>
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<td>Based on the description, distribution, and DNA sequence data on the type series of <em>Indochinella pugio paradoxa</em> (see [23]) (Figure 2(c))</td>
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<td>Unio dolichorhynchus Tapparone-Canefri, 1889</td>
<td><em>Lamellidens corrianus</em> (Lea)</td>
<td>Mercato di Mandalay (L. Fea) [AY-01]</td>
<td><em>Trapezidens dolichorhynchus</em> (Tapparone-Canefri, 1889)</td>
<td>Whereabouts unknown</td>
<td>Based on Prashad’s ([16]: Pl. II, image 11) image of <em>Unio dolichorhynchus</em>, the description, distribution, and DNA sequence data on totopotypes ([24, 30]; this study) (Figure 5(I))</td>
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<td>345</td>
<td>Unio exsolescens [sic.] Gould</td>
<td><em>Trapezoideus exsolescens</em> (Gould)</td>
<td>Meetan, fiume Houngdarau (L. Fea) [HG-01]</td>
<td><em>Trapezoideus mitanensis</em> sp. nov.</td>
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<td>Based on the description, distribution, and DNA sequence on the type series of the new species (this study) (Figures 6(l)–6(n))</td>
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<td>Re-identification by Prashad (1922) (original spelling and authorship)</td>
<td>Modern taxonomic placement</td>
<td>Comments and references</td>
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<td>Unio</td>
<td>Unio feae Tapparone-Canefri, 1889</td>
<td>Parreysisia fiazai (Tapparone-Canefri)</td>
<td>Lamellidens marginalis</td>
<td>Tapparone-Canefri's sample examined; new samples from the Haungthayaw River sequenced (this study) (Figures 3(h) and 3(i)). Based on the description, distribution, and DNA sequence data on new samples from the Haungthayaw River (this study).</td>
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<td>Unio foliaceus Gould</td>
<td>Trapezoideus foliaceus (Gould)</td>
<td>Lamellidens marginalis</td>
<td>Tapparone-Canefri's sample examined; new samples from the locality sequenced (this study) (Figures 6(h)–6(k)). Based on the description, distribution, shell proportions, and new samples from the Haungthayaw River (this study).</td>
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<td>Unio houngdaranicus Tapparone-Canefri, 1889 syn. Nov.</td>
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<td>Unio leoma Benson, 1862</td>
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<td>Unio</td>
<td>Unio margaritae var. hancockii Hanks &amp; Theobald</td>
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<td><em>Unio marginalis</em> var. <em>cylindrica</em> Hanley &amp; Theobald</td>
<td>Mercato di Mandalay (L. Fea)</td>
<td>Lamellidens savadiensis (Nevill, 1877)</td>
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<td>Based on the image of the specimen ([55]: Pl. XLIV, image 1), description and new sequenced samples from the locality (this study)</td>
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<td><em>Unio marginalis</em> var. <em>obesa</em> Hanley &amp; Theobald</td>
<td>Mercato di Mandalay (L. Fea)</td>
<td>Lamellidens savadiensis (Gould, 1847)</td>
<td>Whereabouts unknown</td>
<td>Based on the description, distribution, and DNA sequence data on new samples from Ayeyarwady Basin (this study)</td>
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<td><em>Unio marginalis</em> var. <em>subflabellata</em> Tapparone-Canefri, 1889</td>
<td>Mandalay, del mercato (L. Fea)</td>
<td>Lamellidens savadiensis (Nevill, 1877)</td>
<td>MSNG</td>
<td>Tapparone-Canefri’s sample examined (this study); new samples from the locality sequenced (this study) (Figures 5(e), 5(g), and 5(h))</td>
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<td><em>Unio marginalis</em> var. <em>tricolor</em> Hanley &amp; Theobald</td>
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<td>Lamellidens savadiensis (Nevill, 1877)</td>
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<td><em>Unio marginalis</em> var. <em>zonata</em> Hanley &amp; Theobald</td>
<td>Kokareet, Tenasserim (L. Fea)</td>
<td>Lamellidens savadiensis (Gould, 1847)</td>
<td>Whereabouts unknown</td>
<td>Based on the description, distribution, and DNA sequence data on new samples from the locality (Figure 4(d))</td>
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<td>339</td>
<td><em>Unio Parma</em>, Benson, ex reeve</td>
<td>Meetan, fume Hounghdarau (L. Fea) [HG-01]</td>
<td>Leoparreysia tavoyensis (Gould, 1843)</td>
<td>Whereabouts unknown</td>
<td>Based on the description, distribution, and DNA sequence data on topotypes of <em>Unio Parma</em> from the Tanintharyi River and a sample from the Haungthayaw River (Figure 3(d))</td>
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<td>349</td>
<td><em>Unio protensus</em> Tapparone-Canefri, 1889</td>
<td>Prome, Bassa Birmania (L. Fea)</td>
<td>Trapezidens dolichorhynchus (Tapparone-Canefri, 1889)</td>
<td>Whereabouts unknown</td>
<td>Based on Prashad’s ([16]: Pl. II, image 9) image of <em>Unio protensus</em>, the description, distribution and new sequenced samples (this study) (Figure 5(i))</td>
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<tr>
<td>350</td>
<td><em>Unio protensus</em> var. <em>obtusatus</em> Tapparone-Canefri, 1889</td>
<td>Prome, Bassa Birmania (L. Fea)</td>
<td>Trapezidens dolichorhynchus (Tapparone-Canefri, 1889)</td>
<td>Whereabouts unknown</td>
<td>Based on Prashad’s image of <em>Unio protensus</em> var. <em>obtusatus</em> ([16]: Pl. II, image 10), description, shell proportions, distribution and new sequenced samples (this study) (Figure 5(k))</td>
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<td>350</td>
<td><em>Unio protensus</em> var. <em>marginalis</em> Tapparone-Canefri, 1889</td>
<td>Prome, Bassa Birmania (L. Fea)</td>
<td>Lamellidens savadiensis (Gould, 1847)</td>
<td>MSNG</td>
<td>Based on examined holotype, description, shell proportions, distribution, and new sequenced samples (this study) (Figures 4(e) and 4(f))</td>
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<td>Page</td>
<td>Nominal taxon by Tapparone-Canefri (1889 and collection labels) (original spelling and authorship)</td>
<td>Re-identification by Prashad (1922) (original spelling and authorship)</td>
<td>Label data [old locality code; See Table 1 for detail]</td>
<td>Modern taxonomic placement</td>
<td>Tapparone-Canefri’s sample depository</td>
<td>Comments and references</td>
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<tr>
<td>344</td>
<td><em>Unio pugio</em> Benson, 1862</td>
<td><em>Oxynaia pugio</em> (Benson)</td>
<td>Label: &quot;Mandalay, del mercato&quot; [AY-01]. Published label data: Prome, Bassa Birmania (L. Fea, pochi esemplari) [AY-02]; mercato di Mandalay (L. Fea, esemplari numerosissimi) [AY-01]</td>
<td><em>Indochinella pugio pugio</em> (Benson, 1862)</td>
<td>MSNG</td>
<td>Tapparone-Canefri’s sample examined; new sample from Mandalay sequenced (this study) (Figures 2(a) and 2(b))</td>
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<td>350</td>
<td><em>Unio pulcher</em> Tapparone-Canefri, 1889</td>
<td><em>Lamellidens generosus</em> (Gould)</td>
<td>Tenasserim: Meetan, del fume Houngdarau. Leg. L. Fea [HG-01]</td>
<td><em>Lamellidens generosus</em> (Gould, 1847)</td>
<td>MSNG</td>
<td>Based on the syntypes, description, shell proportions, distribution, and new samples from the type locality (this study) (Figures 4(a) and 4(b))</td>
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<td>351</td>
<td><em>Unio pulcher</em> var. <em>lamelliformis</em> Tapparone-Canefri, 1889</td>
<td><em>Lamellidens generosus</em> (Gould)</td>
<td>Meetan, fume Houngdarau (L. Fea) [HG-01]</td>
<td><em>Lamellidens generosus</em> (Gould, 1847)</td>
<td>Whereabouts unknown</td>
<td>Based on the description, shell proportions, distribution and new samples from the type locality</td>
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<tr>
<td>351</td>
<td><em>Unio pulcher</em> var. <em>ponderosulus</em> Tapparone-Canefri, 1889</td>
<td><em>Lamellidens lamellatus</em> (Lea)</td>
<td>Meetan, fume Houngdarau (L. Fea) [HG-01]</td>
<td><em>Lamellidens generosus</em> (Gould, 1847)</td>
<td>Whereabouts unknown</td>
<td>Based on the description, shell proportions, distribution, and new samples from the type locality</td>
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<td>354</td>
<td><em>Unio rectangularis</em> Tapparone-Canefri, 1889</td>
<td><em>Margaritanopsis laosensis</em> (Lea)</td>
<td>Teinzo, nel fume mule, Monti E. di Bhamo (L. Fea) [AY-05]</td>
<td><em>Yaukthwa rectangularis</em> (Tapparone-Canefri, 1889)</td>
<td>MSNG</td>
<td>Holotype examined [27]; new topotypes sequenced (this study) (Figures 5(d) and 5(e))</td>
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<td>N/A</td>
<td><em>Unio Sella</em> Tapparone-Canefri, unpublished name</td>
<td><em>Margaritanopsis laosensis</em> (Lea)</td>
<td>Carin independ. 1000-1200 m [ST-01]</td>
<td><em>Yaukthwa nesemanni</em> (Konopleva, Bolotov &amp; Kondakov, 2017) (=<em>Unio sella</em> Prashad, 1922; unavailable name, introduced as a synonym)</td>
<td>MSNG</td>
<td>Earlier, the lectotype of <em>Unio sella</em> Prashad, 1922 was designated and examined; topotypes sequenced [24, 28] (Figures 6(a)–6(c))</td>
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<td>343</td>
<td><em>Unio smaragdites</em> Benson, 1862 (this shell is labelled as &quot;Unio scobinatus* Bens.?&quot; in MSNG)</td>
<td><em>Parreyssia smaragdites</em> (Benson)</td>
<td>Label: Mandalay, del mercato [AY-01]. Published label data: Mercato di Mandalay (L. Fea) [AY-01]</td>
<td><em>Indonaia andersoniana</em> (Nevill, 1877)</td>
<td>MSNG</td>
<td>Tapparone-Canefri’s sample examined; new sample from Mandalay sequenced (this study) (Figures 2(j) and 2(k))</td>
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N/A – not available.
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<th>Locality of new sample [old locality code: See Table 1 for detail] (status of sample)</th>
<th>Specimen voucher</th>
<th>GenBank acc. Numbers</th>
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<tr>
<td><em>Unio dolichorhynchus</em> Tapparone-Canefri, 1889</td>
<td><em>Trapezidens dolichorhynchus</em> (Tapparone-Canefri, 1889)</td>
<td>Mandalay [AY-01] (topotype)</td>
<td>RMBH biv 442/2</td>
<td>OL597741 n/a n/a</td>
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<td><em>Unio feae</em> Tapparone-Canefri, 1889 syn. nov.</td>
<td><em>Leoparreyisia tavoyensis</em> (Gould, 1843)</td>
<td>Haungthayaw [close to HG-02] (topotype)</td>
<td>RMBH biv 362/3</td>
<td>MK372425 n/a n/a</td>
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<td><em>Unio generosus</em> var. <em>delapsus</em> Tapparone-Canefri, 1889 syn. nov.</td>
<td><em>Lamellidens generosus</em> (Gould, 1847)</td>
<td>Mitan stream, Haungthayaw Basin [HG-01] (topotype)</td>
<td>RMBH biv 1024/3</td>
<td>OL597808 n/a n/a</td>
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<tr>
<td><em>Unio gianelli</em> Tapparone-Canefri, 1889 syn. nov.</td>
<td><em>Trapezidens dolichorhynchus</em> (Tapparone-Canefri, 1889)</td>
<td>Mandalay [AY-01] (topotype)</td>
<td>RMBH biv 423</td>
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<td><em>Unio gianelli</em> var. <em>degener</em> Tapparone-Canefri, 1889 syn. nov.</td>
<td><em>Trapezidens dolichorhynchus</em> (Tapparone-Canefri, 1889)</td>
<td>Mandalay [AY-01] (topotype)</td>
<td>RMBH biv 417/8</td>
<td>n/a n/a n/a</td>
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<tr>
<td><em>Unio houngdarauicus</em> Tapparone-Canefri, 1889 syn. nov.</td>
<td><em>Leoparreyisia tavoyensis</em> (Gould, 1843)</td>
<td>Haungthayaw [close to HG-02] (topotype)</td>
<td>RMBH biv 362/2</td>
<td>MK372424 n/a n/a</td>
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<td><em>Unio marginalis</em> var. <em>sublabelata</em> Tapparone-Canefri, 1889 syn. nov.</td>
<td><em>Lamellidens savadiensis</em> (Nevill, 1877)</td>
<td>Mandalay [AY-01] (topotypes)</td>
<td>RMBH biv 427A/1 RMBH biv 427A/2</td>
<td>OL597754 n/a n/a OL597755 n/a n/a</td>
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<td><em>Unio protensus</em> Tapparone-Canefri, 1889 syn. nov.</td>
<td><em>Trapezidens dolichorhynchus</em> (Tapparone-Canefri, 1889)</td>
<td>Mandalay [350 km N of AY-02] (non-topotype sample)</td>
<td>RMBH biv 442/1</td>
<td>OL597740 n/a n/a</td>
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<td><em>Unio protensus</em> var. <em>ellipticus</em> Tapparone-Canefri, 1889 syn. nov.</td>
<td><em>Trapezidens dolichorhynchus</em> (Tapparone-Canefri, 1889)</td>
<td>Nyang-U [260 km N of AY-02] (non-topotype sample)</td>
<td>RMBH biv 417/2</td>
<td>MN780886 n/a n/a</td>
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<td><em>Unio protensus</em> var. <em>obtusatus</em> Tapparone-Canefri, 1889 syn. nov.</td>
<td><em>Lamellidens generosus</em> (Gould, 1847)</td>
<td>Pyay [AY-02] (topotypes)</td>
<td>RMBH biv 672/1</td>
<td>OL597804 n/a n/a RMBH biv 672/2 OL597805 n/a n/a</td>
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<td><em>Unio pulcher</em> Tapparone-Canefri, 1889 syn. nov.</td>
<td><em>Lamellidens generosus</em> (Gould, 1847)</td>
<td>Mitan stream, Haungthayaw Basin [HG-01] (topotype)</td>
<td>RMBH biv 1024/1</td>
<td>OL597806 OL598379 n/a n/a</td>
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<td><em>Unio pulcher</em> var. <em>lamellatiformis</em> Tapparone-Canefri, 1889 syn. nov.</td>
<td><em>Lamellidens generosus</em> (Gould, 1847)</td>
<td>Mitan stream, Haungthayaw Basin [HG-01] (topotype)</td>
<td>RMBH biv 1024/5</td>
<td>n/a n/a n/a</td>
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<tr>
<td><em>Unio pulcher</em> var. <em>ponderosus</em> Tapparone-Canefri, 1889</td>
<td><em>Lamellidens generosus</em> (Gould, 1847)</td>
<td>Haungthayaw [close to HG-01] (topotype)</td>
<td>RMBH biv 1024/2</td>
<td>OL597807 n/a n/a</td>
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<th>Locality of new sample [old locality code: See Table 1 for detail] (status of sample)</th>
<th>Specimen voucher</th>
<th>GenBank acc. Numbers</th>
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<tbody>
<tr>
<td><em>Unio rectangularis</em> Tapparone-Canefri, 1889</td>
<td><em>Yaukthwa rectangularis</em> (Tapparone-Canefri, 1889)</td>
<td>Mole stream at Teinthaw village [AY-03] (topotypes)</td>
<td>RMBH biv 916/1  RMBH biv 916/2  RMBH biv 916/3  RMBH biv 917/1</td>
<td>OL597635  OL597636  OL597637  n/a  n/a  OL597638  OL598387  OL598388  OL598389</td>
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<td><em>Unio bonneaudii</em> Tapparone-Canefri, 1889</td>
<td><em>Radiatula mouhoti haungthayawensis</em> Bolotov et al., 2019</td>
<td>Haungthayaw [sample RMBH biv360 close to HG-02 and RMBH biv1023 corresponds to HG-01] (new samples)</td>
<td>RMBH biv 360/1  RMBH biv 360/2  RMBH biv 360/3  RMBH biv 360/10</td>
<td>MK372417  MK372418  MK372419  n/a  MK372493  MK372494  MK372495</td>
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<td><em>Unio coeruleus</em> Tapparone-Canefri, 1889</td>
<td><em>Indonaia andersoniana</em> (Nevill, 1877)</td>
<td>Mandalay [AY-01] (new sample)</td>
<td>RMBH biv 429/1  RMBH biv 361/1  RMBH biv 361/2  RMBH biv 361/3  RMBH biv 356/1  RMBH biv 356/2  RMBH biv 356/3</td>
<td>OL597692  MK372420  MK372421  MK372422  MK372423  MK372424  OL597760  n/a  n/a  OL597761  OL598400  OL598401</td>
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<td><em>Unio crispatus</em> Tapparone-Canefri, 1889</td>
<td><em>Indochinella pugio paradoxa</em> Bolotov et al., 2019</td>
<td>Haungthayaw [close to HG-02] (new sample)</td>
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<td><em>Unio corrianus</em> Tapparone-Canefri, 1889</td>
<td><em>Lamellidens generosus</em> (Gould, 1847)</td>
<td>Mandalay [AY-01] (new sample)</td>
<td>RMBH biv 356/2  RMBH biv 356/3</td>
<td>OL597762  n/a  n/a  OL597763  OL598400  OL598401</td>
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<th>Specimen voucher</th>
<th>GenBank acc. Numbers</th>
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<tr>
<td>Unio exosolescens Tapparone-Canefri, 1889</td>
<td>Trapezoideus mitanesiensis sp. nov.</td>
<td>Mitan stream, Haungthayaw Basin [HG-01] (new sample)</td>
<td>RMBH biv 1021/1</td>
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<td>RMBH biv 1021/3</td>
<td>0L597615 n/a n/a</td>
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<td>Unio foliaceus Tapparone-Canefri, 1889</td>
<td>Yaukthwa zayleymensis (Preston, 1912)</td>
<td>Tarkat stream, Ayeyarwady Basin [100 km N of AY-03] (new sample)</td>
<td>RMBH biv 679/2</td>
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<td>RMBH biv 679/3</td>
<td>OL597658 n/a</td>
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<td>Unio generosus Tapparone-Canefri, 1889</td>
<td>Lamellidens generosus (Gould, 1847)</td>
<td>Mitan stream, Haungthayaw Basin [HG-01] (new sample)</td>
<td>RMBH biv 1024/4</td>
<td>n/a n/a n/a</td>
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<td>Unio leioma Tapparone-Canefri, 1889</td>
<td>Indonaia andersoniana (Nevill, 1877)</td>
<td>Mandalay [AY-01] (new sample)</td>
<td>RMBH biv 434</td>
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<td>Unio marginals Tapparone-Canefri, 1889</td>
<td>Trapezidens dolichorhynchus (Tapparone-Canefri, 1889)</td>
<td>Mandalay [AY-01] (new sample)</td>
<td>RMBH biv 417/3</td>
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<td>Unio marginals var. bilineata Tapparone-Canefri, 1889</td>
<td>Indonaia andersoniana (Nevill, 1877)</td>
<td>Mandalay [AY-01] (new sample)</td>
<td>RMBH biv 429/2</td>
<td>OL597693 n/a n/a</td>
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<td>Unio marginals var. cylindrica Tapparone-Canefri, 1889</td>
<td>Lamellidens savadiensis (Nevill, 1877)</td>
<td>Mandalay [AY-01] (new sample)</td>
<td>RMBH biv 416/3</td>
<td>OL597753 n/a n/a</td>
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<tr>
<td>Unio marginals var. obesa Tapparone-Canefri, 1889</td>
<td>Lamellidens generosus (Gould, 1847)</td>
<td>Mandalay [AY-01] (new sample)</td>
<td>RMBH biv 356/10</td>
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<td>Unio marginals var. tricolor Tapparone-Canefri, 1889</td>
<td>Lamellidens savadiensis (Nevill, 1877)</td>
<td>Mandalay [AY-01] (new sample)</td>
<td>RMBH biv 442/3</td>
<td>OL597756 n/a n/a</td>
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<td>Unio marginals var. zonata Tapparone-Canefri, 1889</td>
<td>Lamellidens generosus (Gould, 1847)</td>
<td>Haungthayaw [close to HG-02] (new sample)</td>
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<td>RMBH biv 364/3</td>
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<td>Unio parma Tapparone-Canefri, 1889</td>
<td>Leoparreysia tavoyensis (Gould, 1843)</td>
<td>Haungthayaw [close to HG-02] (new sample)</td>
<td>RMBH biv 362/1</td>
<td>MK372423 n/a MK372499</td>
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<td>Unio pugio Tapparone-Canefri, 1889</td>
<td>Indochinella pugio pugio (Benson, 1862)</td>
<td>Mandalay [AY-01] (new sample)</td>
<td>RMBH biv 441/2</td>
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</table>
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

## Table 3: Continued.

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<th>Specimen voucher</th>
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<tr>
<td><em>Unio smaragdites</em> Tapparone-Caneffri, 1889</td>
<td><em>Indonaia andersoniana</em> (Nevill, 1877)</td>
<td>Mandalay [AY-01] (new sample)</td>
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**Related nominal taxa**

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<tr>
<td><em>Unio bhamoensis</em> Theobald, 1873</td>
<td><em>Leoparreysia tavoyensis</em> (Gould, 1843)</td>
<td>Bhamo (topotypes)</td>
<td>RMBH biv 266/4</td>
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n/a – not available. Geographic coordinates of each locality are given in Taxonomic account, Table 1 and Table S1.
structure), and Trapezidens dolicoorhynchus (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...
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-Canefri’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. protensis 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. protensis fall into the 95% confidence ellipses of the genus Trapezidens. In turn, Unio gianelli, U. gianelli var. degener, U. protensis var. ellipticus, U. generosus var. delapsus and U. protensis 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+16S rRNA+28S rRNA) revealed 47 species, belonging to 12 genera, i.e. Pseudodon, Monodontina, Sundadontina (Pseudodontini), Trapezoideus, Yaukthwa (Contradentini), Trapezidens, Lamellidens (Lamellidentini), Parreysia (Parreysiini), Leoparreysia...
(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 representatives of a species-level clade corresponding to *Indonaia andersoiana* (Figure S2). Newly collected topotypes of *Unio luteus* Lea, 1856, *U. bhamoensis* Theo bald, 1873, *U. mandelayensis* Theo bald, 1873, *U. feae* Tapparone-Canefri, 1889, and *U. howdgaranicus* 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 Haungthyaw 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 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).
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 Pseudodon 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; Mitian Stream, Haungthayaw Basin). (m) Trapezoideus mitanensis sp. nov. (paratype RMBH 1022/1; Mitian Stream, Haungthayaw Basin). (n) Trapezoideus mitanensis sp. nov. (paratype RMBH 1021/3; Mitian 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).
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


4.1.1. Indochinella 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 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. generous (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.

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)).


= 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. Myadong, 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 and biv 259/3 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.


(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].


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

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


=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.


(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.; 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.; 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.; Ayeyarwady Basin, 13.xii.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 606/5 and biv 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.xii.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,


(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).


=*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.


(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: Mitau 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.


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


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


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


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

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

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


=*Leoparreysia bhamaensis* (Theobald, 1873). – 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 Nyen Chan leg. (Figure 3(d)).

*Unio bhamaensis* Theobald, 1873: syntype NHMUK 88-12-4-1672. Type locality: prope Bhamo Birmanico; necon in Prome occidental Provincia Pegu (Bhamo, Ayeyarwady Basin, Myanmar). Topotypes examined: Myanmar: Myaung Lake near Bhamo, 24.2387°N, 97.1658°E, Ayeyarwady Basin,
and MNHN-IM-2000-38005. Type locality: Meetan, 38002, MNHN-IM-2000-38003, MNHN-IM-2000-38004 and ZSI M17512 (Figure 3(h)), syntypes MNHN-IM-2000-M11965/2 (note on the label: Exchange from Geneva Mus.)

Vikhrev, and Nyein Chan leg. (Figure 3(g)).

447, including biv 447/1 and biv 447/2 sequenced), Bolotov, upstream of Kawkareik town, 16.4714°, 09.i.i.2018, 1 specimen (RMBH biv 362/2, sequenced), Bolotov, Vikhrev, and Nyein Chan leg. (Figure 3(i)).

Topotypes examined: Myanmar: Ayeyarwady River, upstream of Kawkareik town, 16.4714°, 09.i.i.2018, 1 specimen (RMBH biv 362/2, sequenced), Bolotov, Vikhrev, and Nyein Chan leg. (Figure 3(i)).


Type locality: Meetan, fiume Houngdarau (Mitan Stream, Haungthayaw River, Myanmar). Topotypes examined: Myanmar: Haungthayaw River upstream of Kawkareik town, 16.4714°, 09.i.i.2018, 1 specimen (RMBH biv 362/2, sequenced), Bolotov, Vikhrev, and Nyein Chan leg. (Figure 3(i)).

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: Mian Stream, 16.9770°N, 97.6330°E, Salween Basin, 11.i.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.i.2018, 11 specimens (RMBH biv 425, including biv 425/1 and biv 425/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Ayeyarwady River near the former Newville village, 17.0292°N, 97.9043°E, 1 specimen (RMBH biv 363/2, sequenced), Nyein Chan leg. (Figure 3(i)).

(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.


4.5.1. 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 var. ponderosus Tapparone-Canefri, 1889: 351 [15].

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


=Unio protensis 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)).


=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 MZCU 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 635, including biv 635/1, biv 635/2 and biv 635/3 sequenced), Than Win leg. (Figure 4(c)).

locality: Meetan, fiume Hountydarau (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)).


(7) Distribution. Endemic to Myanmar: widespread throughout the Ayeyarwady (including Chindwin), Bago, Sittaung, Lower Salween, Haungthayaw, Haingbwe, 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* (Annan-dale, 1918) (=*Physunio microproteroides* Annandale, 1918) [56]. In turn, *Unio pulcher* var. *lamelliformis*, *U. pulcher* var. *ponderosulus*, and *U. generosus* var. *delapsus* described from Mitan Stream, Haungthaway 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. *sublabellata* Tapparone-Canefri, 1889: 346 [15] (new junior synonym) (Figures 5(e), 5(g), 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)).


(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.


4.6.1. *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)).
354 \[15\] (new junior synonym).

Type species: \textit{Trapezoidea nesemanni} (Konopleva, Bolotov & Kondakov, 2017). – Bolotov et al., 2017: 13 [24].


\textit{=Margaranopsis laensis} Prashad, 1922: 93 [16] (identification error) [28].

\textit{=Trapezoidea nesemanni} Konopleva, Bolotov \& Kondakov, 2017. – Bolotov et al., 2017: 13 [24].


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

(3) Type Material Examined. The type series of \textit{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 “\textit{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.; Ayeyarwady River at Mandalay, 21.9909°N, 96.0610°E, 04.iii.2018, 2 specimens (RMBH biv 422/1 and biv 422/2 sequenced), Bolotov, Nyein Chan, and Vikhrev leg.; Ayeyarwady River at Mandalay city market, approx. 21.9491°N, 96.0483°E, 02.iii.2018, 1 specimen (RMBH biv 144/14, biv 144/25 and biv 255/3).

4.7.2. Yaukthwa rectangularis (Tapparone-Canefri, 1889).

=Unio rectangularis Tapparone-Canefri (1889): 354 [15].

=Unio dalliana Bolotov et al., 2019: Supplementary Table 1 [23] (identification error).
=Indonaia rectangularis (Tapparone-Canefri, 1889). – Bolotov et al., 2019: 25 [27].

(1) Type. Holotype (by monotypy) labelled “Unio rectangularis Tapp. Can. Teinz. Mit E. di Bhamo (L. Fea)” (MSNG; examined by us).
(2) Type Locality. Teinz, nel fume Mule, Monti E. di Bhamo (Mole Stream (Mole Chaung in Burmese) near Teintaw 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), Ney Chin 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.; Nuniuinhka 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, Ney Chin, Vikhrev, Kondakov, and Gofarov leg.; Mogau 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, Ney Chin, Vikhrev, Kondakov, and Gofarov leg.; Mogau 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, Ney Chin, Vikhrev, Kondakov, and Gofarov leg.; Nantin 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, Ney Chin, 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. dallylana (see [20, 23]) is in fact Y. rectangularis. Furthermore, sequenced topotypes of Yaukthwa dallylana 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)).

=itrapezoideus foliaceus var. zayleymanensis Preston, 1912: 307 [50].
=Yaukthwa zayleymanensis (Preston, 1912). – Konопleva 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 Zayleymen (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), Bolotov, Ney Chin leg. (Figure 6(i)).
(4) Tapparone-Canefri’s Material Examined. One shell in MSNG labelled “Unio foliaceus Gould var. fragilis
4.8. Genus Trapezoideus Simpson, 1900 (Subfamily Gonideinae


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.


(7) Description. Shell small, trapezoidal, thin, moderately inflated, rounded anteriorly, 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 wrinkles. Area from umbo along dorsal margin covered by fine wrinkles. 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 attachment scars very shallow or reduced.


(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*.


= *Pseudodon kayinensis* Bozlot 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.


(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 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 unreliability of 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 paradoxia*, *Indonaia andersoniana*, *Lamellidens generous*, *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 Leandro 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 Tapparone-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 substitutions 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 toptotypes 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 periostracular or even structure of the teeth (Figure 3). Until today these taxa were not subjected by detailed taxonomic revision. *Unio luteus* was synonymized 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*, *Leguminia 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 (Genidea angulata, Leguminaea whealtleyi, 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 S5. 3 codons of COI+16S rRNA sequence alignment. Alignment S2. COI sequence alignment of Indochenillini 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)

References


[54] C. T. Simpson, A Descriptive Catalogue of the Naiades, or Pearly Fresh-Water Mussels (Parts I-III), Bryant Walker, Detroit, 1914.


