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*, *Radiatula chaudhuri*, *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 Leopar-Reysia tayovenesis (Gould, 1843), Trapezidens dolichor-hynchus (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.wsu.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,
as well as the sculpture and periostracum [17, 20]. We analyzed 88 contours of the Lamellidentini representatives, i.e. *Lamellidens generous*, *L. savadiensis*, and *Trapezidens dolicchorhynchus*, 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
Margaritiferidae, i.e. Gibbosa laoensis (Lea, 1863) and Margaritifera dahurica (Middendorf, 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 independent runs of 25 × 10⁶ 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 Lamellidentina, Leoparreysiina, Indochniella, 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 as stated above, but for BI analysis two independent runs of 25 × 10⁶ 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 paradoxo, Indonaia andersoniana, Radiana chaudhuri and R. mouhoti haunghayawensis (Figure 2), Leoparreysia tavoyensis (Figure 3), Lamellidens generous (Figure 4), L. savadiensis and Trapezidens dolichorhynchus (Figure 5), Yaukthwa nesenmanni 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.

| Code   | Original label(s) | Locality data                                                                 | Approximate geographic coordinates | References                  |
|--------|-------------------|--------------------------------------------------------------------------------|-------------------------------------|-----------------------------|
| HG-01  | Tenasserim: Meetan, fiume Hougndarau | Mitran stream (Mitran Chaung in Burmese), a tributary of the upstream section of the Haunghtayaw River, Myanmar | Latitude: 15.9999 Longitude: 98.3946 | Tapparone-Canefri [15]      |
| HG-02  | Kokareet, Tenasserim | A stream at Kawkairek town, Haunghtayaw Basin, Myanmar | Latitude: 16.5528 Longitude: 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 | Latitude: 21.9491 Longitude: 96.0483 | Tapparone-Canefri [15]      |
| AY-02  | Prome, Bassa Birmania | Ayeyarwady River at Pyay city, Myanmar | Latitude: 18.8142 Longitude: 95.2138 | Tapparone-Canefri [15]      |
| AY-03  | Teinzo del mule Chaung; Teinzo, N. E. di Bham; Teinzo, nel fiume mule, Monti E. di Bhamo; A(lta). Birmania: Teinzo | Mole stream (mole Chaung in Burmese) at Teinthaw village, Ayeyarwady Basin, Myanmar | Latitude: 24.3978 Longitude: 97.2519 | Tapparone-Canefri [15]; Bolotov et al. [27] |
| ST-01  | Carin independ. 1000-1200 m | Upstream section of the Tauk Ue Kupt River, Sittauing Basin, Myanmar | Latitude: 19.3075 Longitude: 96.7219 | Bolotov et al. [28]          |
| 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: Teinzò 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 toptype ([24, 30]; this study) (Figure 5(l)) |
| 345  | *Unio exsolescens* [sic.] Gould                                                                  | *Trapezoideus exsolescens* (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. |
|---------------------|
| **Nominal taxon by Tapparone-Canefri (1889 and collection labels) (original spelling and authorship)** |
| **Modern taxonomic placement** |
| **Comments and references** |
| **Page** |
| **Unio jousi* Tapparone-Canefri, 1889** |
| *Unio jousi* Tapparone-Canefri, 1889 (original spelling and authorship) |
| Based on the description, distribution, and DNA sequence data on new samples from Mandalay (this study) (Figures 2(l) and 2(m)). |
| 340 |
| **Unio jousi** var. *delapsus* Tapparone-Canefri, 1889 |
| Lamellidens jousi var. delapsus (Gould) |
| Mercato di Mandalay (L. Fea) [AY-01] |
| Whereabouts unknown |
| Based on the description, distribution, and shell proportions (Figure 5(m)). |
| 341 |
| **Unio jousi** var. *fossor* Tapparone-Canefri, 1889 |
| Lamellidens jousi var. fossor (Gould) |
| Mercato di Mandalay (L. Fea) [AY-01] |
| Whereabouts unknown |
| Based on the description, distribution, and shell proportions (Figure 5(m)). |
| 342 |
| **Unio jousi** var. *oblongus* Tapparone-Canefri, 1889 |
| Lamellidens jousi var. oblongus (Gould) |
| Mercato di Mandalay (L. Fea) [AY-01] |
| Whereabouts unknown |
| Based on the description, distribution, and shell proportions (Figure 5(m)). |
| 343 |
| **Unio jousi** var. *spinosus* Tapparone-Canefri, 1889 |
| Lamellidens jousi var. spinosus (Gould) |
| Mercato di Mandalay (L. Fea) [AY-01] |
| Whereabouts unknown |
| Based on the description, distribution, and shell proportions (Figure 5(m)). |
| 344 |
| **Unio jousi** var. *tomentosus* Tapparone-Canefri, 1889 |
| Lamellidens jousi var. tomentosus (Gould) |
| Mercato di Mandalay (L. Fea) [AY-01] |
| Whereabouts unknown |
| Based on the description, distribution, and shell proportions (Figure 5(m)). |
| 345 |
| **Unio jousi** var. *tuberculatus* Tapparone-Canefri, 1889 |
| Lamellidens jousi var. tuberculatus (Gould) |
| Mercato di Mandalay (L. Fea) [AY-01] |
| Whereabouts unknown |
| Based on the description, distribution, and shell proportions (Figure 5(m)). |
| 346 |
| **Unio jousi** var. *xylocodon* Tapparone-Canefri, 1889 |
| Lamellidens jousi var. xylocodon (Gould) |
| Mercato di Mandalay (L. Fea) [AY-01] |
| Whereabouts unknown |
| Based on the description, distribution, and shell proportions (Figure 5(m)). |
| 347 |
| **Unio jousi** var. *xylothyrum* Tapparone-Canefri, 1889 |
| Lamellidens jousi var. xylothyrum (Gould) |
| Mercato di Mandalay (L. Fea) [AY-01] |
| Whereabouts unknown |
| Based on the description, distribution, and shell proportions (Figure 5(m)). |
| 348 |
| 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) | MSNG | 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) | MSNG | Based on the description, distribution, and DNA sequence data on new samples from Ayeyawady 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)) |
| 346  | *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, fume Hounghdarau (L. Fea) [HG-01] | Leoparreyssia 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].                              | *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 fume 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. lamelliformis Tapparone-Canefri, 1889 *Lamellidens generosus* (Gould)      | Meetan, fume 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. ponderosus Tapparone-Canefri, 1889 *Lamellidens lamellatus* (Lea)          | Meetan, fume 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 laoensis* (Lea)                  | Teinzo, nel fume 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 laoensis* (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) | Label: Mandalay, del mercato [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.
| 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 |
|----------------|---------------------------|--------------------------------------------------------------------------------|------------------|--------------------|
| **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 generousus 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 gianellii 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 427A/1 | OL597754 n/a n/a |
| *Unio marginalis var. subflabellata* Tapparone-Canefri, 1889 syn. nov. | *Lamellidens savadiensis* (Nevill, 1877) | Mandalay [AY-01] (topotypes) | 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 |
| *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 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 |
| 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 |
|-----------------|-----------------------------|----------------------------------------------------------------------------------|------------------|---------------------|
| *Unio rectangularis*  
Tapparone-Canefri, 1889 | *Yaukthwa rectangularis*  
(Tapparone-Canefri, 1889) | Mole stream at Teinthaw village [AY-03] (topotypes) | RMBH biv 916/1  
OL597635  
ON142664  
OL598387 | COI  
16S rRNA  
28S rRNA |
| *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 360/3  
MK372419  
n/a  
MK372495 | RMBH biv 1026/3 |
| *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 356/1  
OL597761  
n/a  
OL598400 |
| *Unio crispatus*  
Tapparone-Canefri, 1889 | *Indochinella pugio paradoxa*  
Bolotov et al., 2019 | Haungthayaw [close to HG-02] (new sample) | RMBH biv 361/2  
MK372421  
MK372466  
MK372497 | RMBH biv 356/2  
OL597762  
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 260/9  
MF352331  
MF352391 | RMBH biv 260/10 |
| *Unio coeruleus*  
Tapparone-Canefri, 1889 | *Indonaia andersoniana*  
(Nevill, 1877) | Mandalay [AY-01] (new sample) | RMBH biv 429/1  
OL597692  
n/a  
n/a | RMBH biv 429/1  
OL597692  
n/a  
n/a |
| *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 1026/1  
OL597610  
n/a  
n/a |
| *Unio corianus*  
Tapparone-Canefri, 1889 | *Lamellidens generosus*  
(Gould, 1847) | Mandalay [AY-01] (new sample) | RMBH biv 356/2  
OL597762  
n/a  
n/a | RMBH biv 356/2  
OL597762  
n/a  
n/a |

Taxonomic opinions of Tapparone-Canefri [15]
| 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 |
|-------------------------|---------------------------|-----------------------------------------------------------------------------------|------------------|---------------------|
| *Unio exsolescens*      | *Trapezoideus mitanensis* sp. nov. | Mitan stream, Haungthayaw Basin [HG-01] (new sample) | RMBH biv 1021/1  | OL597613 OL142670 ON171238 |
| *Unio foliaceus*        | *Yaukthwa zayleymansensis* (Preston, 1912) | Tarkat stream, Ayeyarwady Basin [100 km N of AY-03] (new sample) | RMBH biv 679/2  | MN275075 MN307262 MN307204 |
| *Unio generosus*        | *Lamellidens generosus* (Gould, 1847) | Mitan stream, Haungthayaw Basin [HG-01] (new sample) | RMBH biv 1024/4  | n/a n/a n/a |
| *Unio leiona*           | *Indonaia andersoniana* (Nevill, 1877) | Mandalay [AY-01] (new sample) | RMBH biv 434  | OL597695 n/a n/a |
| *Unio marginalis*       | *Trapezidens dolichorhynchus* (Tapparone-Canefri, 1889) | Mandalay [AY-01] (new sample) | RMBH biv 417/3  | MN780887 n/a n/a |
| *Unio marginalis* var.  | *Indonaia andersoniana* (Nevill, 1877) | Mandalay [AY-01] (new sample) | RMBH biv 429/2  | OL597693 n/a n/a |
| *bilineata* Tapparone-Canefri, 1889 | | | | |
| *Unio marginalis* var.  | *Lamellidens savadiensis* (Nevill, 1877) | Mandalay [AY-01] (new sample) | RMBH biv 416/3  | OL597753 n/a n/a |
| *cylindrica* Tapparone-Canefri, 1889 | | | | |
| *Unio marginalis* var.  | *Lamellidens generosus* (Gould, 1847) | Mandalay [AY-01] (new sample) | RMBH biv 356/10 | n/a n/a n/a |
| *obesa* Tapparone-Canefri, 1889 | | | | |
| *Unio marginalis* var.  | *Lamellidens savadiensis* (Nevill, 1877) | Mandalay [AY-01] (new sample) | RMBH biv 442/3  | OL597756 n/a n/a |
| *tricolor* Tapparone-Canefri, 1889 | | | | |
| *Unio marginalis* var.  | *Lamellidens generosus* (Gould, 1847) | Haungthayaw [close to HG-02] (new sample) | RMBH biv 363/1  | OL597768 n/a OL598403 |
| *zonata* Tapparone-Canefri, 1889 | | | | |
| *Unio parma*            | *Leoparreysia tavoyensis* (Gould, 1843) | Haungthayaw [close to HG-02] (new sample) | RMBH biv 362/1  | MK372423 n/a MK372499 |
| Tapparone-Canefri, 1889 | | | | |
| *Unio pugio*            | *Indochinella pugio pugio* (Benson, 1862) | Mandalay [AY-01] (new sample) | RMBH biv 441/2  | n/a n/a n/a |
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
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...
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. 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+16S rRNA+28S rRNA) revealed 47 species, belonging to 12 genera, i.e. Pseudodon, Monodontina, Sundadontina (Pseudodontini), Trapezoideus, Yaukthwa (Contradentini), Trapezidens, Lamellidens (Lamellidontini), Parreysia (Parreysiini), Leoparreysia

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; Hlaingwwe 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 bhanoensis 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).
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 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 (Ayeyawady 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 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, Ayeyawady 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, Ayeyawady 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; 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 (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 totopotypes of other nominal Tapparone-Canefri’s taxa were also phylogenetically divided among representatives of the Indochinellini, Leoparreysiini, Lamelli- dentini, 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* (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)).
(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, 24.2965°N, 96.4746°E, Kachin State, Ayeyarwady Basin, 10.ii.2017, 7 specimens (RMBH biv 332), Nyen Chan leg.; Ayeyarwady River, 24.2965°N, 96.4746°E, Kachin State, Ayeyarwady Basin, 10.ii.2017, 7 specimens (RMBH biv 332), Nyen

Figure 8: Maximum likelihood phylogeny of the complete data set of mitochondrial and nuclear sequences (five partitions: three codons of COI+16S rRNA+28S 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.
Lea, 1831 (by original designation).

Type species: *Vikhrev & Konopleva, 2018*.

Henderson, 1935, Tribe Indochinellini Bolotov, Pfeiffer, Vikhrev & Konopleva, 2018).

4.2. Genus Indonaia Prashad, 1918 (Subfamily Parreysiinae Henderson, 1935, Tribe Indochinellini Bolotov, Pfeiffer, Vikhrev & Konopleva, 2018). Type species: *Unio caerulesus* 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)).

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

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

= *Unio 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 259/2 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. XXVI. 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(ai). 1886. L. Fea!”; one shell in MSNG labelled “*Unio scobinatus* Bens.? Det. Tapp. Mandalay, del mercato. Dic(embre). 1885 – Genn(ai). 1886. L. Fea!”; One shell in MSNG labelled “*Unio scobinatus* Bens.? Det. Tapp. Mandalay, del mercato. Dic(embre). 1885 – Genn(ai). 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, Sittauung 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, Sittauung 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 Gofarow 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].
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 bonneaudi* 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.i.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 chaudhuri* (Preston, 1912) and *Indonaia bonneaudi* (Eydoux, 1838).
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 generous (Gould, 1847). = *Unio generous* 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: 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 homonym 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 635, including biv 635/1, biv 635/2 and biv 635/3 sequenced), Bolotov, Vikhrev, and Nyein Chan leg.; Tanintharyi River, 12.0914°N, 98.2183°E, 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)).

(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.; Ayeyarwady River, 25.0352°N, 96.5885°E, 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), Bolotov, Vikhrev, and 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. bhanoensis* 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*. 
locality: Meetan, fiume Houngdarau (Mita 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 vari.). Bassa Birmania: Prome, negli argini della città, marzo 1886. Leg. L. Fea! Tapp. Ann. M. C. Gen. XXVII, 1889, p. 347. Manda- lay, del mercato. Dicembre. 1885-1886. Leg. L. Fea!"

(5) Tapparone-Canefri's Non-Type Material Examined. One shell in MSNG labelled "*Unio corinunus*, Lea. Tapp. Ann. M. C. Gen. XXVII, 1889, p. 347. Manda- lay, del mercato. Dicembre. 1885-1886. 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.; Kalemno 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 Kalemno, 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.; Moeyungyi Lake, 17.5968’N, 96.5950’E, 17.ii.2018, 10 specimens (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.; Kyaunk 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.; Pathhein river, 17.4567’N, 97.1850’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 other species, *Lamellidens ferrugineus* (Annandale, 1918) (=Physunio micropteroides Annandale, 1918) [56]. In turn, *Unio pulcher* var. *lammelatiformis*, *U. pulcher* var. *ponderosus*, and *U. generosus* var. *delapsus* described from Mitan Stream, Maungthaway 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, 24.2972° 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 varietà!). Mandala, del mercato, Dic(embre). 1885 – Genn(aio). 1886. Leg. L. Fea!” Type locality: Mandala, del mercato (Mandala 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. Mandala, 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.ii.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.ii.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 gianellii 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) (Ayeayarwady River at Mandalay city (bought in a city market), approx. 21.9941°N, 96.0483°E, Myanmar).

(3) Topotypes Examined. Myanmar: Ayeayarwady 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.; Ayeayarwady River at Thar Kone village, 21.3145°N, 95.05889°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.; Ayeayarwady 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, 23.1499°N, 94.1434°E, Ayeayarwady 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, Ayeayarwady 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.

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

(5) Other Material Examined. Myanmar: Ayeayarwady 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.; Ayeayarwady River at Mandalay city, 21.9941°N, 96.0483°E, Myanmar.

(6) Distribution. Endemic to Myanmar: widespread throughout the Ayeayarwady 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, Ayeayarwady 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.; Ayeayarwady River at Mandalay, 21.9574°N, 96.0510°E, 03.iii.2018, 1 specimen (RMBH biv 437 sequenced), Bolotov, Nyein Chan, and Vikhrev leg.; Ayeayarwady 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, 96.0819°E, Ayeayarwady Basin, 14.xi.2018, 15 specimens (RMBH biv 612 and biv 613 (only 5 tissue snips), including biv 612/1, biv 612/2, biv 613/1, biv 613/2 and biv 613/3 sequenced), Bolotov, Vikhrev, Lopes-Lima, Bogan, and Nyein Chan leg.; Indaw River near Sell Ywar village, 24.2123°N, 96.0819°E, Ayeayarwady River, 14.xi.2018, 15 specimens (RMBH biv 612 and biv 613 (only 5 tissue snips), including biv 612/1, biv 612/2, 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, Ayeayarwady, 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...
4.7.2. **Yaukthwa rectangularis** (Tapparone-Canefri, 1889).

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

=*Margaritansopsis 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, Figure 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.; Namuinhka 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.; Moguang 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.; Moguang 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*”
Neve A. Birmania: Teinzio. L. Fea!" (Mole Stream near Teinthaw village, 24.3978’N, 97.2519’E, Ayeyarwady Basin, Myanmar) (Figures 6(i) 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.xxii.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, 2 specimens (RMBH biv 917/2 and 917/3 sequenced, Bolotov, Vikhrev, 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, Kon-dakov, 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 Model. 1942). Type species: Unio foliaceus Gould, 1843 (by original designation).

4.8.1. Trapezoideus mitanensis Bolotov, Konopleva, Than Win, Kondakov & Vikhrev Sp. Nov. =Unio exolescens (sic) Tapparone-Canefri, 1889: 345 [15] (identification error and incorrect spelling of Unio exolescens Gould, 1843; sampling locality: Meean, fume Houndgara (Mitan Stream, 15.999’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: OLS97613 (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 G, 319 C, 336 C), and a substitution in the nuclear 28S rRNA gene (620 C).

(7) Description. Shell small, trapezoidal, thin, moderately inflated, rounded anteriodorally, 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.

(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: Indochenella pugio pugio, I. pugio paradoxa, Indonaia andersoniana, Lamellidens generous, L. savadiensis, Leoparreysia tavoyensis, Pseudodon kayinensis, Radiatula chaudhurii, R. mouthoi haungthayawensis, Trapezidens dolichorhynchus, Yaukthwa zayleymanensis, Y. rectangularis, and Trapezoideus mitanensis sp. nov. A relatively low species richness in Leonard 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 Contraentini [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 periostracum 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. *Indonaiia andersoniana*, *Indochinella pugio pugio*, and *Lamellidens generous*, 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 Unionoidae 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 Leoparreysini 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 (Genidea angulata, Leguminia wheatsleyi, Potomidia 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+16S rRNA+28S rRNA sequence alignment. Alignment S2. COI sequence alignment of Indochninellini from Myanmar. Alignment S3. COI sequence alignment of Leoparreyisini 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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