A taxonomic review of *Trapezidens* (Bivalvia: Unionidae: Lamellidentini), a freshwater mussel genus endemic to Myanmar, with a description of a new species

EKATERINA S. KONOPLEVA1*, IVAN N. BOLOTOV1, ALEXANDER V. KONDAKOV1, OLEG D. KONONOVA1, MIKHAIL YU. GOFAROV1, ALENA A. TOMILOVA1, ZAU LUN2, THAN WIN3 & ILYA V. VIKHREV1

1Federal Center for Integrated Arctic Research, Russian Academy of Sciences, 163000, Arkhangelsk, Russia
2Fauna & Flora International – Myanmar Program, Yangon, Myanmar
3Department of Zoology, Dawei University, Dawei, Tanintharyi Region, Myanmar
*Corresponding author: es.konopleva@gmail.com

Received 23 November 2019  |  Accepted by V. Pešić: 2 January 2020  |  Published online 12 January 2020.

Abstract

*Trapezidens* Bolotov, Vikhrev & Konopleva, 2017 (Bivalvia: Unionidae: Lamellidentini) is a peculiar freshwater mussel genus, the range of which is confined to the Western Indochina Subregion (Myanmar). Here we show that this genus contains five allopatric species: *Trapezidens angustior* (Hanley & Theobald, 1876) from the Bago, Sittaung, and Bilin rivers; *T. dolichorhynchus* (Tapparone-Canefri, 1889) from the Ayeyarwady River; *T. exolescens* (Gould, 1843) from the Bago River; *T. scutum* (Sowerby, 1868) from the Tanintharyi (Great Tenasserim) River; and *T. yeti* sp. nov. from the Ye River. Phylogenetically, *Trapezidens angustior, T. dolichorhynchus*, and *T. yeti* sp. nov. are closely related to each other, forming a species complex, while *T. exolescens* and *T. scutum* represent the most distant lineages within the genus. An updated synonymy for each species is compiled.

Key words: *Trapezidens*, endemic taxa, new species, Western Indochina.

Introduction

Southeast Asia is one of the most species-rich hotspots of freshwater mussel diversity worldwide (Bolotov et al. 2017a, b, 2018, 2019a; Lopes-Lima et al. 2017; Pfeiffer et al. 2018; Zieritz et al. 2018; Konopleva et al. 2019). The genus *Trapezidens* Bolotov, Vikhrev & Konopleva, 2017 (Bivalvia: Unionidae: Lamellidentini) was established for a small group of freshwater mussels endemic to Myanmar (Bolotov et al. 2017b). Representatives of this genus were recorded from the Ayeyarwady, Bago, Bilin, Dawei, Sittaung, Tanintharyi (Great Tenasserim), and Ye rivers (Konopleva et al. 2017; Bolotov et al. 2017b; this study). Although recent research revealed that this genus may contain at least three valid species (Bolotov et al. 2017b), its taxonomy has not yet been studied in detail. It was found that several mussel-associated leech species (Hirudinea: Glossiphoniidae) use *Trapezidens* species as a secondary host and shelter (Bolotov et al.
TAXONOMIC REVIEW OF FRESHWATER MUSSEL GENUS TRAPEZIDENS

2019b), whereas other ecological features of these freshwater mussels such as habitats and life cycle are almost unknown.

This study aims to revise the genus *Trapezidens* by an integrative approach and to describe a new species recently collected from the Ye River in southeastern Myanmar.

Materials and methods

The specimens of *Trapezidens* species, including topotypes, and the type specimens of *Trapezidens yeti* sp. nov. were studied in the malacological collection of the Russian Museum of Biodiversity Hotspots (RMBH thereafter), Federal Center for Integrated Arctic Research of the Russian Academy of Sciences, Arkhangelsk, Russia. These samples were collected throughout Myanmar during 2015-2018, and the topotypes of all nominal taxa belonging to the genus *Trapezidens* were located (Fig. 1).

![Distribution and the type localities of *Trapezidens* species in Myanmar.](image)

**Figure 1.** Distribution and the type localities of *Trapezidens* species in Myanmar. The numbers on the map indicate the type localities (green stars) and ranges (color filling) of certain species as follows: (1) *Trapezidens yeti* sp. nov.: Ye River basin. (2) *T. scutum*: Tanintharyi (Great Tenasserim) River basin. (3) *T. angustior*: Bago (Pegu), Sittaung, and Bilin river basins. (4) *T. exolescens*: Dawei (Tavoy) River basin. (5) *T. dolichorhynchus*: Ayeyarwady (Irrawaddy) River basin.
Comparative analyses of the shell morphology were carried on the shell shape, umbo position, the pseudo-cardinal, and lateral teeth structures, and muscle attachment scars (Konopleva et al. 2019).

The length, height, and width of the shell (all at the maximum diameter) of each specimen from the new species were measured using dial calipers (±0.1 mm).

Molecular analyses, including DNA extraction, PCR, sequencing, sequence checking, and alignment followed Bolotov et al. (2017b). New sequences of the mitochondrial cytochrome c oxidase subunit I (COI), small ribosomal RNA (16S rRNA), and the nuclear large ribosomal RNA (28S rRNA) gene fragments from Trapezidens samples including the new species were generated and deposited in NCBI GenBank (Tables 1-2). Sequences of four Lamellidens species were added to the dataset as in-group taxa, i.e. L. savadiensis (Nevill, 1877), L. generosus (Gould, 1847), L. ferrugineus (Annandale, 1918), and L. marginalis (Lamarck, 1819) (Table 1). Sequences of Leoparreysia species, i.e. L. olivacea (Prashad, 1930), L. canefrii Vikhrev, Bolotov & Kondakov, 2017, and L. tavoyensis (Gould, 1843), were used as outgroup (Table 1).

### Table 1. List of molecular sequences used in this study.

| Species               | Locality                                      | Specimen Voucher No.* | NCBI's GenBank acc. nos. |
|-----------------------|-----------------------------------------------|------------------------|--------------------------|
| **Trapezidens yeti sp. nov.** | Myanmar: Ye River                           | RMBH biv 616_1         | MN780888 MN79081 MN79085 |
|                       |                                               | RMBH biv 616_2         | MN780889 MN79082 MN79086 |
|                       |                                               | RMBH biv 617_1         | MN780890 MN79083 MN79087 |
|                       |                                               | RMBH biv 617_2         | MN780891 MN79084 MN79088 |
| **T. yeti sp. nov.**   | Myanmar: Ye River                           | RMBH biv 250_4         | MF352238 MF352308 MF352366 |
|                       |                                               | RMBH biv 250_7         | MF352239 MF352309 MF352367 |
|                       |                                               | RMBH biv 250_8         | MF352240 MF352310 MF352368 |
|                       | Myanmar: Sittaung River basin, Myit Kyi Pauk Stream | RMBH biv 255_1       | MF352235 MF352320 MF352378 |
| **T. angustior**       | Myanmar: Sittaung River basin, Myit Kyi Pauk Stream | RMBH biv 394_1     | MN275088 n/a n/a |
|                       | Myanmar: Sittaung River basin, Chain Stream | RMBH biv 394_3       | MN780885 n/a n/a |
|                       | Myanmar: Bilin River                         | RMBH biv 370_1         | MN275087 MN307273 MN307215 |
|                       | Myanmar: Bilin River                         | RMBH biv 370_2         | MN780875 n/a n/a |
|                       | Myanmar: Bilin River                         | RMBH biv 370_3         | MN780876 n/a n/a |
|                       | Myanmar: Bago River                          | RMBH biv 382_1         | MN780877 n/a n/a |
|                       | Myanmar: Bago River                          | RMBH biv 382_2         | MN780878 n/a n/a |
|                       | Myanmar: Bago River                          | RMBH biv 382_3         | MN780879 n/a n/a |
|                       | Myanmar: Bago River basin, Moload Stream     | RMBH biv 385_1         | MN780880 n/a n/a |
|                       | Myanmar: Bago River basin, Kyak Phar Stream  | RMBH biv 387_3         | MN780881 n/a n/a |
|                       | Myanmar: Bago River basin, Kyak Phar Stream  | RMBH biv 388_1         | MN780882 n/a n/a |
|                       | Myanmar: Bago River basin, Kyak Phar Stream  | RMBH biv 388_2         | MN780883 n/a n/a |
|                       | Myanmar: Bago River basin, Kyak Phar Stream  | RMBH biv 388_3         | MN780884 n/a n/a |
| **T. dolichorhynchus** | Myanmar: Ayeyarwady River                   | UA 20729.1            | JN243903 KP795042 JN243881 |
|                       | Myanmar: Ayeyarwady River basin, Myit Tha (Manipur) River | RMBH biv 336_1 | MN780869 n/a n/a |

..continued on the next page
| Table 1 |
|-----------------------------------------------|
| **T. dolichorhynchus** | Myanmar: Ayeyarwady River basin, Myit Tha (Manipur) River | RMBH biv 336_2 | MN780870 | n/a | n/a |
| **T. dolichorhynchus** | Myanmar: Ayeyarwady River basin, Myit Tha (Manipur) River | RMBH biv 336_3 | MN275090 | n/a | MN307217 |
| **T. dolichorhynchus** | Myanmar: Ayeyarwady River basin, Chindwin River | RMBH biv 353 | MN780871 | n/a | n/a |
| **T. dolichorhynchus** | Myanmar: Ayeyarwady River basin, Chindwin River | RMBH biv 354_1 | MN780872 | n/a | n/a |
| **T. dolichorhynchus** | Myanmar: Ayeyarwady River basin, Chindwin River | RMBH biv 354_2 | MN780873 | n/a | n/a |
| **T. dolichorhynchus** | Myanmar: Ayeyarwady River basin, Chindwin River | RMBH biv 354_3 | MN780874 | n/a | n/a |
| **T. dolichorhynchus** | Myanmar: Ayeyarwady River near Tant Kyi village | RMBH biv 417_1 | MN275089 | MN307274 | MN307216 |
| **T. dolichorhynchus** | Myanmar: Ayeyarwady River near Tant Kyi village | RMBH biv 417_2 | MN780886 | n/a | n/a |
| **T. dolichorhynchus** | Myanmar: Ayeyarwady River near Tant Kyi village | RMBH biv 417_3 | MN780887 | n/a | n/a |
| **T. exolescens** | Myanmar: Dawei River | RMBH biv 145_3 | KX230532 | KX230548 | KX230559 |
| **T. exolescens** | Myanmar: Dawei River | RMBH biv 145_12 | KX230535 | KX230549 | KX230560 |
| **T. exolescens** | Myanmar: Dawei River | RMBH biv 145_21 | KX230536 | KX230550 | KX230561 |
| **T. exolescens** | Myanmar: Dawei River | RMBH biv 146_11 | KX230537 | KX230551 | KX230562 |
| **T. exolescens** | Myanmar: Dawei River | RMBH biv 146_14 | KX230539 | n/a | n/a |
| **T. exolescens** | Myanmar: Dawei River | RMBH biv 146_23 | KX230540 | KX230552 | KX230563 |
| **T. scutum** | Myanmar: Tanintharyi River basin, Nga Wun River | RMBH biv 630_1 | MN275084 | MN307270 | MN307212 |
| **T. scutum** | Myanmar: Tanintharyi River basin, Nga Wun River | RMBH biv 630_2 | MN275085 | MN307271 | MN307213 |
| **T. scutum** | Myanmar: Tanintharyi River basin, Nga Wun River | RMBH biv 632_1 | MN275086 | MN307272 | MN307214 |
| **T. scutum** | Myanmar: Tanintharyi River basin, Nga Wun River | RMBH biv 632_2 | MN780892 | n/a | n/a |
| **T. scutum** | Myanmar: Tanintharyi River basin, Nga Wun Stream | RMBH biv 644 | MN780893 | n/a | n/a |
| **T. scutum** | Myanmar: Tanintharyi River basin, Nga Wun Stream | RMBH biv 645_1 | MN780894 | n/a | n/a |
| **Lamellidens savadiensis** | Myanmar: Irrawaddy River basin, Lake Indawgyi | RMBH: biv109_1 | KX230544 | KX230555 | KX230566 |
| **L. generosus** | Myanmar: Sittaung River basin, Pathi River | RMBH: biv242_3 | MF352219 | MF352293 | MF352351 |
| **L. ferrugineus** | Myanmar: Salween River basin, lower channel of Lake Inle | RMBH: biv113_8 | KX865825 | KX865596 | KX865699 |
| **L. marginalis** | Myanmar: Kaladan River basin, unnamed puddle | RMBH: biv 153 | KX230547 | KX230558 | KX230569 |
| **Leoparreysia olivacea** | Myanmar: Ayeyarwady River basin | UMMZ:304641 | KP795022 | KP795044 | KP795005 |
| **L. canefrii** | Myanmar: Sittaung River near Taungoo | RMBH biv 249 | MF352237 | MF352307 | MF352365 |
| **L. tavoyensis** | Myanmar: Tavoy River | RMBH biv 149 | KX230543 | KX230554 | KX230565 |

*RMHB – Russian Museum of Biodiversity Hotspots, Federal Center for Integrated Arctic Research, Russian Academy of Sciences, Arkhangelsk, Russia. **These species were used as outgroup. n/a – not available.
Phylogenetic analyses were performed based on the combined data set of Lamellidetini (COI + 16S rRNA + 28S rRNA) with 49 sequences collapsed into 31 unique haplotypes (Table 1). Maximum likelihood phylogenetic searches were carried out using the web interface and server for IQ-TREE (W-IQ-TREE) with GTR+G model for each partition (Nguyen et al. 2015; Chernomor et al. 2016; Trifinopoulos et al. 2016). An ultrafast bootstrap algorithm (UFBoot) with 5,000 replicates was applied to estimate the probability of internal branches (Hoang et al. 2017). Mean uncorrected COI p-distance to the sister species was calculated using MEGA 7 (Kumar et al. 2016). The molecular diagnosis of the new species was designed as described in Bolotov et al. (2017b, 2019).

Table 2. Shell measurements and reference DNA sequences for the type series of *Trapezidens yeti* sp. nov.

| Status of specimen | Specimen Voucher No.* | Shell length, mm | Shell height, mm | Shell width, mm | NCBI’s GenBank acc. nos. |
|-------------------|-----------------------|------------------|------------------|-----------------|------------------------|
| Holotype          | RMBH biv 616_1        | 55.8             | 26.6             | 15.0            | MN780888, MN759081, MN759085 |
| Paratype          | RMBH biv 616_2        | 50.9             | 26.7             | 13.3            | MN780889, MN759082, MN759086 |
| Paratype          | RMBH biv 616_3        | 48.8             | 26.4             | 14.2            | n/a, n/a, n/a           |
| Paratype          | RMBH biv 616_4        | 64.2             | 31.7             | 16.3            | n/a, n/a, n/a           |
| Paratype          | RMBH biv 616_5        | 46.2             | 23.1             | 12.2            | n/a, n/a, n/a           |
| Paratype          | RMBH biv 617_1        | 45.7             | 24.3             | 12.3            | MN780890, MN759083, MN759087 |
| Paratype          | RMBH biv 617_2        | 41.3             | 20.9             | 11.2            | MN780891, MN759084, MN759088 |
| Paratype          | RMBH biv 617_3        | 49.6             | 23.9             | 13.1            | n/a, n/a, n/a           |
| Paratype          | RMBH biv 617_4        | 48.8             | 24.7             | 12.7            | n/a, n/a, n/a           |
| Paratype          | RMBH biv 617_5        | 42.6             | 21.6             | 10.8            | n/a, n/a, n/a           |
| Paratype          | RMBH biv 617_6        | 48.2             | 24.1             | 13.5            | n/a, n/a, n/a           |
| Paratype          | RMBH biv 617_7        | 45.6             | 22.9             | 12.2            | n/a, n/a, n/a           |
| Paratype          | RMBH biv 617_8        | 46.6             | 23.6             | 12.9            | n/a, n/a, n/a           |
| Paratype          | RMBH biv 617_9        | 47.8             | 24.4             | 12.1            | n/a, n/a, n/a           |
| Paratype          | RMBH biv 617_10       | 44.1             | 22.0             | 11.7            | n/a, n/a, n/a           |
| Paratype          | RMBH biv 675_1        | 46.3             | 23.1             | 12.8            | MN780895, n/a, n/a      |
| Paratype          | RMBH biv 675_2        | 47.8             | 23.6             | 13.2            | MN780896, n/a, n/a      |
| Paratype          | RMBH biv 675_3        | 48.5             | 24.8             | 12.5            | n/a, n/a, n/a           |

*RMBH – Russian Museum of Biodiversity Hotspots, Federal Center for Integrated Arctic Research, Russian Academy of Sciences, Arkhangelsk, Russia. n/a – not available.

Results

Our multi-locus phylogeny and morphological data indicate that the genus *Trapezidens* contains five species: *T. angustior* (Hanley & Theobald, 1876), *T. dolicorhynchus* (Tapparone-Canefri, 1889), *T. exolescens* (Gould, 1843), *T. scutum* (Sowerby, 1868), and *T. yeti* sp. nov. The ranges of these species correspond to the allopatric speciation model (Fig. 1). The new species belongs to a species complex containing *Trapezidens angustior* and *T. dolicorhynchus*. The two other species in this genus, i.e. *Trapezidens scutum* and *T. exolescens* represent two divergent phylogenetic lineages (Fig. 2).

Morphological studies demonstrate that *Trapezidens* species can be distinguished from each other by shell shape and general outlines (Fig. 3). The hinge and muscle attachment scars structure in all *Trapezidens* species are typical for the genus, and the development of these features primarily depends on the shell size. Young specimens of *Trapezidens angustior* resemble those of *Lamellidens* species based on the shell shape, while older specimens share a smoother shell outline without a marked wing. *Trapezidens dolicorhynchus* is the largest representative of the genus with an elongated and thick shell, strong pseudocardinal teeth and deep muscle attachment scars. *Trapezidens scutum* has a rather large shell with well-developed conchological traits. Its specific feature among other *Trapezidens* taxa is the presence of small granules on the umbo cavity surface. *Trapezidens exolescens* and *T. yeti* sp. nov. are the smallest representatives of the genus and morphologically are very similar to each other, whereas phylogenetically they represent distant lineages. All five species appear to be taxa endemic to the Western Indochina Subregion.
Figure 2. Phylogenetic tree recovered from Maximum likelihood analysis of the combined data set of mitochondrial and nuclear sequences of the Lamellidentini (five partitions: three codons of COI + 16S rRNA + 28S rRNA). Leoparreysia species were used as outgroup (not shown). Scale bar indicates the branch lengths. Black numbers near nodes are values of Ultrafast Bootstrap Support (UBS). Trapezidens yetì sp. nov. is colored red.

Taxonomic account

Family Unionidae Rafinesque, 1820
Subfamily Parreysiinae Henderson, 1935
Tribe Lamellidentini Modell, 1942
Genus Trapezidens Bolotov, Vikhrev & Konopleva, 2017

Trapezidens angustior (Hanley & Theobald, 1876)
Fig. 3a
=Unio generous var. angustior Hanley & Theobald (1876): 22, Pl. 46, Fig. 7. Type locality: Pegu [Bago River, Myanmar]. Type: Holotype BMNH_1968655 [by monotypy]; Natural History Museum, London, UK (examined by us).
=Lamellidens marginalis var. sublamellatus Preston (1912): 305; Preston (1915): 181, Fig. 19. Type locality: Burma. Type: Holotype M4711 [by original designation]; Zoological Survey of India, Kolkata, India (fide Ramakrishna et al. 2004) (not examined by us). The holotype is listed in the Catalogue of the type specimens of the Mollusca section of the Zoological Survey of India (Ramakrishna et al. 2004). This nominal taxon has been assigned to T. angustior based on conchological features of the holotype, i.e. the elongate-rectangular shell shape, specific structure of the pseudocardinal teeth, and clear radial lines on the outer side of the valve (Preston 1915: Fig. 19).
=Trapezidens obesa angustior (Hanley & Theobald, 1876). – Bolotov et al. (2017b): 10.
=Trapezidens obesa feae Kondakov, Konopleva & Vikhrev in Bolotov et al. (2017b): 8, Fig. 3d. Type locality: Myanmar: Sittaung, Myit Kyi Pauk Stream. Types: Holotype NCSM 103035 [by original designation; transferred from RMBH biv 250_4]; North Carolina Museum of Natural Sciences, Raleigh, USA (examined by us). Paratypes NCSM 103029 (transferred from RMBH biv 250_3 and biv 250_7), RMBH biv 250_8. This taxon is considered a synonym of T. angustior based on molecular sequence data.
Figure 3. Shells of five *Trapezidens* species: a) *T. angustior* [topotype RMBH biv 382_3]; b) *T. dolichorhynchus* [topotype RMBH biv 417_2]; c) *T. exolescens* [topotype RMBH biv 145_12]; d) *T. scutum* [topotype RMBH biv 632_1]; e) *T. yeti* sp. nov. [holotype RMBH biv 616_1]. Scale bar = 20 mm. (Photos: Ekaterina S. Konopleva).
Topotypes examined. MYANMAR: Bago River, 17.5334°N, 96.3315°E, 18.ii.2018, 11 specimens [RMBH biv 382, including specimens biv 382_1, biv 382_2, and biv 382_3 being sequenced], Bolotov, Nyein Chan and Vikhrev leg.

Other material examined. MYANMAR: Myit Kyi Pauk Stream, 18.9613°N, 96.4455°E, Sittaung River basin, 26.11.2016, 4 specimens [NCSM 103029 (transferred from RMBH biv 250_3 and biv 250_7), NCSM 103035 (transferred from biv 250_4), and RMBH biv 250_8; the three latter specimens are sequenced], Vikhrev leg.; Thauk Ye Kupt River, 18.9840°N, 96.4361°E, Sittaung River basin, 26.xi.2016, 1 specimen [RMBH biv 255_1, sequenced], Vikhrev leg; Bilin River, 17.3306°N, 97.2418°E, 13.ii.2018, 5 specimens [RMBH biv 370, including specimens RMBH biv 370_1, biv 370_2, and biv 370_3 being sequenced], Bolotov, Nyein Chan and Vikhrev leg.; Chain Stream, 17.9769°N, 96.7659°E, Sittaung River basin, 20.ii.2018, 5 specimens [RMBH biv 394_1, biv 394_2, biv 394_5, biv 394_6, biv 394_7, and biv 394_8; the two latter specimens are sequenced], Bolotov, Nyein Chan and Vikhrev leg.; Molod Stream, 17.6011°N, 96.2861°E, Bago River basin, 18.ii.2018, 5 specimens [RMBH biv 385_1, biv 385_5, biv 385_6, biv 385_8, biv 385_9; the first specimen is sequenced], Bolotov, Nyein Chan and Vikhrev leg.; Kyak Phar Stream, 17.6660°N, 96.2465°E, Bago River basin, 19.ii.2018, 17 specimens [RMBH biv 385_9; the first specimen is sequenced], Bolotov, Nyein Chan and Vikhrev leg.; Moload Stream, 17.6011°N, 96.2465°E, Bago River basin, 20.ii.2018, 5 specimens [RMBH biv 387_1, biv 387_4, biv 387_6, biv 387_8, biv 387_9, biv 387_10, biv 388 (nos. 4-10), biv 387_3, biv 388_1, biv 388_2, biv 388_3; the four latter specimens are sequenced], Bolotov, Nyein Chan and Vikhrev leg.

Differential diagnosis. Shell rhomboid and somewhat winged in young specimens (similar to that in Lamellidens species) to elliptical and elongated in adult mussels, inequilateral, slightly inflated and moderately thick. In the process of shell growth, the dorsal margin becomes smooth and almost parallel to the ventral margin, posterior slope maybe biangular or truncated. Adult specimens are very similar to Tapparone (Hanley & Theobald 1876). However, an expanded dataset reveals that this taxon has a broader range and is conspecific with Tapparone angustior that was described from the Bago River (Hanley and Theobald 1876).

Distribution. Endemic to the Bago, Sittaung, and Bilin rivers, Myanmar.

Comments. Previously, we described Tapparone obesa feae as a subspecies-level lineage endemic to the Sittaung River (Bolotov et al. 2017b). However, an expanded dataset reveals that this taxon has a broader range and is conspecific with Tapparone angustior that was described from the Bago River (Hanley and Theobald 1876).
Topotypes examined. MYANMAR: Ayeyarwady River near Tant Kyi village, 21.1567°N, 94.8050°E, 02.iii.2018, 16 specimens [RMBH biv 417, including specimens RMBH biv 417_1, biv 417_2, and biv 417_3 being sequenced], Bolotov, Nyein Chan and Vikhrev leg.

Other material examined. MYANMAR: Myit Tha (Manipur) River, 23.22845°N, 94.1434°E, Ayeyarwady River basin, 02.ii.2018, 6 specimens [RMBH biv 336, including specimens RMBH biv 336_1, biv 336_2, and biv 336_3 being sequenced], Bolotov, Nyein Chan and Vikhrev leg; Chindwin River, 23.1499°N, 94.3627°E, Ayeyarwady River basin, 04.ii.2018, 7 specimens [RMBH biv 353 and biv 354, including specimens RMBH biv 353, biv 354_1, biv 354_2, and biv 354_3 being sequenced], Bolotov, Nyein Chan and Vikhrev leg.

Differential diagnosis. Shell large, very elongated, inequilateral, irregularly elliptic with slightly curved or straight ventral margin and slightly raised dorsal margin, rather thick and moderately inflated. Periostracum dark-brown with well visible growth lines. Pseudocardinal teeth massive, lateral teeth long and sharp, mussel scars deep.

Molecular diagnosis. *Trapezidens dolichorhynchus* is closely related to *T. angustior* and *T. yeti* sp. nov. (mean uncorrected COI p-distances: 2.14% and 1.96% respectively), but it can be distinguished from the sister species by two fixed substitutions in the COI gene fragment as follows: 479 T and 569 G; two fixed substitutions in 16S rRNA gene fragment as follows: 186 T and 196 C.

Distribution. Endemic to the Ayeyarwady River, Myanmar.

Comments. Phylogenetically and morphologically, specimens from the Ayeyarwady, Chindwin, and Manipur rivers do not have any significant differences. Our novel results support the morphology-based hypothesis that the nominal taxa *Trapezidens dolichorhynchus* (Ayeyarwady) and *Unio scutum* var. *humi*ior (Chindwin and Manipur) are conspecific (Bolotov et al. 2017b).

*Trapezidens exolescens* (Gould, 1843)

Fig. 3c

=Unio exolescens Gould (1843): 141. Type locality: Tavoy, Burmah [Dawei River]. Type: Lectotype USNM_85473 [selected by R.I. Johnson, 1964]; National Museum of Natural History, Washington, USA (examined by us).

=Trapezoideus exolescens (Gould, 1843). – Simpson (1900): 859.

=Lamellidens exolescens (Gould, 1843). – Konopleva et al. (2017): 204.

=Trapezidens exolescens (Gould, 1843). – Bolotov et al. (2017b): 7.

Topotypes examined. MYANMAR: Dawei (Tavoy) River, 14.5013°N, 98.1558°E, 26.iv.2015, 51 specimens [lots RMBH biv 145 and biv 146, including specimens RMBH biv 145_3, biv 145_6, biv 145_11, biv 145_12, biv 145_21, biv 146_2, biv 146_7, biv 146_11, biv 146_14, biv 146_20, and biv 146_23 being sequenced], local fishermen leg.

Differential diagnosis. Shell rather small, trapezoidal, compressed and thin, with a slightly variable dorso-anterior margin that is higher and more oblique in adult musse.ls. Periostracum olive-brown to grey-brown. The species differs from its congeners by well-developed anterior and posterior muscle attachment scars even in young specimens. Pseudocardinal teeth small, oblique; lateral teeth parallel to the dorsal margin.

Molecular diagnosis. *Trapezidens exolescens* is closely related to *T. scutum* (mean uncorrected COI p-distance: 3.56%), but it can be distinguished from the sister species by eight fixed substitutions in the COI gene fragment as follows: 29 G, 47 A, 107 C, 122 G, 155 T, 158 C, 419 C and 554 C; two fixed substitutions in 16S rRNA gene fragment as follows: 318 A and 430 A; one fixed substitution in 28S rRNA gene fragment – 701 C, as well as deletion from 582 to 587 positions.

Distribution. Endemic to the Dawei River, Myanmar.

Comments. This species was thought to be widespread across Southeast and South Asia (Zieritz et al. 2018) but later considered a single-drainage endemic species with a restricted range (Bolotov et al. 2017b; Konopleva et al. 2017, 2019).

*Trapezidens scutum* (Sowerby, 1868)

Fig. 3d

=Unio scutum Sowerby (1868): Pl. 94, sp. 510. Type locality: Tenasserim. Type: Holotype BMNH_1907-10-28-239 [by monotypy]; Natural History Museum, London, UK (examined by us).

=Lamellidens scutum (Sowerby, 1868). – Simpson (1900): 857; Konopleva et al. (2017): 210.

=Trapezidens scutum (Sowerby, 1868). – Bolotov et al. (2017b): 10.
Topotypes examined. MYANMAR: Nga Wun River, 11.8567°N, 99.1181°E, Tanintharyi River basin, 25.xi.2018, 4 specimens [RMBH biv 630_1, biv 632_1, biv 630_2 (ethanol-preserved tissue snip only), and biv 632_2 (ethanol-preserved tissue snip only); all sequenced], Bolotov, Nyein Chan and Vikhrev leg.; Nga Wun Stream, 11.8233°N, 99.14934°E, Tanintharyi River basin, 2 specimens [RMBH biv 644 and biv 645_1; all sequenced], Nyein Chan leg.

Differential diagnosis. Shell rhomboid, winged posteriorly, inequilateral, moderately thick and inflated. Periostracum dark-brown to black. Pseudocardinal teeth strong, anterior tooth smaller, posterior tooth bigger, somewhat leaf-like, ribbed. Umbo cavity deeper than that in other Trapezidens species, with small granules on its surface.

Molecular diagnosis. Trapezidens scutum is closely related to T. exolescens (mean uncorrected COI p-distance: 3.56%), but it can be distinguished from the sister species by nine fixed substitutions in the COI gene fragment as follows: 68 A, 134 C, 179 C, 308 A, 335 G, 443 C, 638 A, 647 C and 653 T; three fixed substitutions in 16S rRNA gene fragment as follows: 14 G, 285 C, and 335 G.

Distribution. Endemic to the Tanintharyi (Great Tenasserim) River, Myanmar.

Comments. Previously, we assumed that Trapezidens scutum may be conspecific with T. exolescens based on the proximity of their ranges and conchological similarity (Konopleva et al. 2017). However, this hypothesis was not supported by the novel molecular data, because these taxa represent two divergent phylogenetic lineages.

Trapezidens yeti sp. nov.
Figs. 3e, 4
https://zoobank.org/urn:lsid:zoobank.org:act:CE1C5610-AB1F-4E46-BEA4-4C466B109963

Holotype RMBH biv 616_1: MYANMAR: Ye River near Kyaung Ywar village, 15.2957°N, 97.9984°E, 20.xi.2018, Nyein Chan and Vikhrev leg.

Paratypes. The same locality, date and collectors, 14 specimens [RMBH biv 616_2, biv 617_1, biv 617_2, biv 616_3, biv 616_4, biv 616_5, biv 617_3, biv 617_4, biv 617_5, biv 617_6, biv 617_7, biv 617_8, biv 617_9, biv 617_10; the three first specimens are sequenced]; Ye River, 15.2957°N, 97.9984°E, 2018, 3 specimens [RMBH biv 675, including specimens RMBH biv 675_1 and biv 675_2 being sequenced], Than Win leg.

Etymology. The name of the new species refers to the Ye River, its type locality.

Differential diagnosis. Morphologically, specimens of the new species, especially young mussels, can hardly be distinguished from Trapezidens exolescens. Adult specimens differ from other congeners by a more elongated shell with wider anterior margin and usually without prominently winged dorsal margin, and by peculiar curved pseudocardinal teeth in the right valve.

Molecular diagnosis. Phylogenetically, Trapezidens yeti sp. nov. is closely related to T. angustior and T. dolichorhynchus (mean uncorrected COI p-distances: 1.87% and 1.96% respectively), forming a species complex, but it can be distinguished from the sister species by five fixed substitutions in the COI gene fragment as follows: 257 A, 314 G, 344 C, 413 A, and 614 T; two fixed substitutions in 16S rRNA gene fragment as follows: 382 C and 488 C.

Description. A rather small mussel, with shell length 41.3–64.2 mm, shell height 20.9–31.7 mm, and shell width 10.8–16. 3 mm. Shell somewhat trapezoidal, elongated, inequilateral, thin and not inflated. Anterior margin rounded, ventral margin usually straight, dorsal margin slightly curved, posterior slope diagonally truncated. Umbo small, slightly elevated under hinge line, eroded. Periostracum brownish, sometimes with darker posterior margin. Thin radial lines cross the shell from the umbo area to the ventral margin. Dorsal margin sometimes has small ridges. Nacre whitish with dark-yellow areas, which may almost cover the entire inner side. Two pseudocardinal teeth on the right valve, posterior tooth strong and well-developed, the anterior tooth usually smaller and lamellar. On the left valve, one elongated pseudocardinal tooth with a cavity and a triangular edge. Lateral teeth elongated, one on the right valve and two on the left valve. Anterior muscle scars bean-like, pronounced, posterior muscle scars rounded and less developed.

Distribution. Endemic to the Ye River, Myanmar.
Discussion

This small correspondence is the following step towards a complete revision of the Unionidae from Myanmar. Based on previous works (Bolotov et al. 2017a, 2017b, 2018, 2019a; Konopleva et al. 2017, 2019), the taxonomic concept for this area has shifted from a few widespread species crossing a variety of freshwater basins to multiple species with restricted ranges and endemic to a single drainage basin or even to a section within a freshwater system.

The genus Trapezidens was established for a distant Lamellidentini clade containing members of the so-called exolescens-group (Konopleva et al. 2017; Bolotov et al. 2017b). Initially, we assumed that this genus may contain at least three valid species (Bolotov et al. 2017b). However, further broad-scale sampling of these peculiar mussels throughout Myanmar with a special focus on the type localities of nominal taxa indicates that there are five allopatric Trapezidens species. The range of Trapezidens angustior crosses several river drainages, i.e. the Bago, Sittaung, and Bilin rivers. Trapezidens dolichorrhynchus is restricted to the massive Ayeyarwady River system, with exception of its upstream tributaries (e.g. north of Putao) having a stony bottom and strong current with multiple rapids and waterfalls. In contrast, the three other species are confined to smaller freshwater basins, i.e. Trapezidens exolescens is endemic to the Dawei River, T. scutum to the Tanintharyi (Great Tenasserim) River, and T. yeti sp. nov. to the Ye River. Interestingly, all Trapezidens species were recorded from flowing water, while taxa in their sister genus Lamellidens strongly prefer lacustrine environments, being typical inhabitants of lakes, reservoirs, fishponds, and stagnant ditches. Previously, we proposed that Trapezidens exolescens and T. scutum may be conspecific based solely on conchological features (Konopleva et al. 2017). However, newly collected topotypes of Trapezidens scutum share distant molecular sequences supporting the status of this taxon as a valid species. The small granules on the umbo cavity surface are considered here as a diagnostic feature for this peculiar species. The new
species, *Trapezidens yeti* sp. nov., was collected from the Ye River, which is directly adjacent to the Dawei River, where *T. exolescens* was found. Based on the proximity of those river systems and morphological similarity, we initially considered the sample from the Ye River as representatives of *Trapezidens exolescens*, but later they were found as two distant phylogenetic lineages, sharing another remarkable example of convergence in conchological traits.

Finally, future studies of *Trapezidens* species must be focused on their biological and ecological patterns, i.e. fish hosts, life cycles, and habitat requirements. This information is urgently needed to estimate the conservation status of these species.

**Acknowledgements**

This study was supported by the Ministry of Science and Higher Education of Russia, the Ministry of Europe and Foreign Affairs of France (MEAE), and the Ministry of Higher Education, Research and Innovation of France (MESRI) under project No. 05.616.21.0114 of the Hubert Curien Partnership (PHC) for the Franco-Russian Cooperation for Science and Technology (PHC Kolmogorov 2019). The work was carried out with the support and equipment of the Russian Museum of Biodiversity Hotspots, N. Laverov Federal Center for Integrated Arctic Research, Russian Academy of Sciences, a unique scientific setting (www.ckp-rf.ru/usu/352654). We are grateful to the late Dr. Tony Whitten (Fauna & Flora International – Asia-Pacific, UK), Mr. Frank Momberg (Director for Program Development and Asia-Pacific Program Director of Fauna & Flora International, UK), Mr. Mark Grindley (Country Director of Fauna & Flora International – Myanmar Program, Myanmar), and the staff of the Department of Fisheries of the Ministry of Agriculture, Livestock and Irrigation of Myanmar for their great help during this study. Our research in Myanmar has been performed under the survey permission No. 5/6000/LFR(210/2018) issued by the Ministry of Agriculture, Livestock and Irrigation of Myanmar and the export permission No. NWCD/CITES/9/5666/2018 issued by the Forest Department of the Ministry of Environmental Conservation and Forestry of Myanmar. We would like to thank two anonymous reviewers for their valuable comments and corrections which helped to improve earlier versions of this paper.

**References**

Bolotov, I.N., Kondakov, A.V., Vikhrev, I.V., Aksenova, O.V., Bespalaya, Y.V., Gofarov, M.Y., Kolosova, Y.S., Konopleva, E.S., Spitsyn, V.M., Tannmuangpak, K. & Tumpeesuwan, S. (2017a) Ancient river inference explains exceptional Oriental freshwater mussel radiations. *Scientific Reports*, 7, 1–14.

Bolotov, I.N., Vikhrev, I.V., Kondakov, A.V., Konopleva, E.S., Aksenova, O.V., Gofarov, M.Y. & Tumpeesuwan, S. (2017b) New taxa of freshwater mussels (Unionidae) from a species-rich but overlooked evolutionary hotspot in Southeast Asia. *Scientific Reports*, 7, 1–18.

Bolotov, I.N., Pfeiffer, J., Konopleva, E.S., Vikhrev, I.V., Kondakov, A.V., Aksenova, O.V., Gofarov, M.Yu., Tumpeesuwan, S., Win, T. (2018) A new genus and tribe of freshwater mussel (Unionidae) from Southeast Asia. *Scientific Reports*, 8, 1–12.

Bolotov, I.N., Konopleva, E.S., Vikhrev, I.V., Lopes-Lima, M., Bogan, A.E., Zau Lunn, Nyein Chan, Than Win, Aksenova, O.V., Gofarov, M.Yu., Tomilova, A.A. & Kondakov, A.V. (2019a) Eight new freshwater mussels (Unionidae) from tropical Asia. *Scientific Reports*, 9, 1–15.

Bolotov, I.N., Klass, A.L., Kondakov, A.V., Vikhrev, I.V., Bespalaya, Y.V., Gofarov, M.Y., Filippov, B.Y., Bogan, A.E., Lopes-Lima, M., Zau Lunn, Nyein Chan, Aksenova, O.V., Dvorevkin, G.A., Chapurina, Y.E., Kim, S.K., Kolosova, Y.S., Konopleva, E.S., Lee, J.H., Makhrov, A.A., Palatov, D.M., Sayenko, E.M., Spitsyn, V.M., Sokolova, S.E., Tomilova, A.A., Than Win, Zubrii, N.A. & Vinarski, M.V. (2019b) Freshwater mussels house a diverse mussel-associated leech assemblage. *Scientific Reports*, 9, 1–22.

Chernomor, O., von Haeseler, A. & Minh B. Q. (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology*, 65, 997–1008.

Gould, A. A. (1843) Dr. Gould had examined the shells not long since announced as having been received from the Rev. Francis Mason, missionary at Tavoy, in British Burmah. *Proceedings of the Boston Society of Natural History*, 1, 139–141.

Hanley, S. & Theobald, W. (1876) *Conchologia Indica: Illustrations of the Land and Freshwater Shells of British India*. London, L. Reeve & Co., 65 pp.
Hoang D. T., Chernomor O., von Haeseler A., Minh B. Q. & Vinh L. S. (2017) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35, 518–522.

Konopleva E.S., Bolotov, I. N., Vikhrev I.V., Gofarov, M.Y., Kondakov, A.V. (2017) An integrative approach underscores the taxonomic status of Lamellidens exolescens, a freshwater mussel from the Oriental tropics (Bivalvia: Unionidae). *Systematics and Biodiversity*, 15(3), 204–217.

Konopleva, E.S., Pfeiffer, J.M., Vikhrev, I.V., Kondakov, A.V., Gofarov, M.Yu., Aksenova, O.V., Lunn, Z., Chan, N., Bolotov, I. N. (2019) A new genus and two new species of freshwater mussels (Unionidae) from western Indochina. *Scientific Reports*, 9, 1–14.

Kumar, S., Stecher, G., & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33, 1870–1874.

Lopes-Lima, M., Froufe, E., Do, V.T., Ghamizi, M., Mock, K.E., Kebapçi, Ü., Klishko, O., Kovitvadhı, S., Kovitvadhı, U., Paulo, O.S., Pfeiffer III, J.M., Raley, M., Riceardi, N., Şereflışan, H., Sousa, R., Teixeira, A., Varandas, S., Wu, X., Zanatta, D.T., Zieritz, A. & Bogan, A.E. (2017) Phylogeny of the most species-rich freshwater bivalve family (Bivalvia: Unionida: Unionidae): Defining modern subfamilies and tribes. *Molecular Phylogenetics and Evolution*, 106, 174–191.

Martens, E. v. (1899) Binnen-Conchylien aus Ober-Birma. *Archiv für Naturgeschichte*, 65, 30–48.

Nguyen, L.-T., Schmidt, H. A., Haeseler, von, A. & Minh, B. Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32, 268–274.

Pfeiffer, J. M., Graf, D. L., Cummings, K. S. & Page, L. M. (2018) Molecular phylogeny and taxonomic revision of two enigmatic freshwater mussel genera (Bivalvia: Unionidae incertae sedis: *Harmandia* and *Unionetta*) reveals a diverse clade of Southeast Asian Parreysiinae. *Journal of Molluscan Studies*, 84, 404–416.

Prashad, B. (1922) A revision of the Burmese Unionidae. *Records of the Indian Museum*, 24, 91–111.

Preston, H.B. (1912) A catalogue of the Asiatic naiades in the collection of the Indian Museum, Calcutta, with descriptions of new species. *Records of the Indian Museum*, 7, 279–308.

Preston, H.B. (1915) *Mollusca (Freshwater Gastropoda & Pelecypoda). Fauna of British India, including Ceylon and Burma*. London, Taylor & Francis, 244 pp.

Ramakrishna, Dey, A. & Mitra, S.C. (2004) Catalogue of type species (Bivalvia, Scaphopoda) present in the Mollusca section of Zoological Survey of India. *Records of the Zoological Survey of India (Occasional Paper)*, 228, 1–97.

Simpson, C.T. (1900) Synopsis of the naiades, or pearly fresh-water mussels. *Proceedings of the United States National Museum*, 22, 501–1044.

Sowerby, G.B. (1868) Genus *Unio. Conchologica Iconica*, 16, 61–96.

Tapparone-Canefri, C. (1889) Viaggio de Leonardo Fea in Birmania e regioni vicine. XVIII. Molluschi terrestri e d’acqua dolce. *Annali del Museo Civico di Storia Naturale de Genova (series 2)*, 27, 295–359.

Trifinopoulos, J., Nguyen, L. T., von Haeseler, A. & Minh, B. Q. (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, 44, W232–W235.

Zieritz, A., Bogan, A.E., Froufe, E., Klishko, O., Kondo, T., Kovitvadhı, U., Kovitvadhı, S., Lee, J. H., Lopes-Lima, M., Pfeiffer, J. M., Sousa, R., Do, T. V., Vikhrev, I. & Zanatta, D.T. (2018) Diversity, biogeography and conservation of freshwater mussels (Bivalvia: Unionida) in East and Southeast Asia. *Hydrobiologia*, 810, 29–44.