Phylogeography and distribution of the freshwater razor clams *Novaculina myanmarensis* and *N. gangetica* in Myanmar, with notes on two doubtful nominal taxa described as *Novaculina* members (Bivalvia: Pharidae)

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Abstract
The razor clam genus *Novaculina* Benson, 1830 (Bivalvia: Pharidae: Pharellinae) is a group of secondary freshwater bivalves. Four allopatric species in this genus are distributed throughout Asian freshwater drainages from the Ganges River in India to the Yangtze River in China. Here, we present several new occurrences of *Novaculina myanmarensis* and *N. gangetica* from Myanmar that were confirmed by means of a molecular approach. These occurrences expand our knowledge on the ranges of both species. Furthermore, we compiled an updated distribution map for all the species in this genus. Our phylogeographic research suggests that *Novaculina myanmarensis* colonized the Ayeyarwady Basin from rivers of the Salween Estuary (Donthami and Ataran rivers) during the Late Pleistocene. Conversely, *Novaculina gangetica* populations from Myanmar does not demonstrate any clear phylogeographic structure. At first glance, this pattern can also be caused by a (sub)recent (Pleistocene) immigration into coastal rivers of western Myanmar from the Ganges Basin, although this preliminary hypothesis is yet to be confirmed using DNA sequences of samples from India and Bangladesh. Finally, the taxonomic status of two doubtful nominal taxa initially described as *Novaculina* members is discussed, i.e. *N. gangetica theobaldi* Hanley & Theobald, 1874 and *N. andamanensis* Preston, 1908. These taxa are considered junior subjective synonyms of the estuarine bivalve species *Cultellus maximus* (Gmelin, 1791) (Pharidae) and *Azorinus coarctatus* (Gmelin, 1791) (Solecurtidae), respectively.

Key words: Freshwater bivalves, freshwater biogeography, Southeast Asia, Indo-Myanmar biodiversity hotspot, Ayeyarwady River, Salween Estuary, COI gene, Pleistocene, dispersal events.
Introduction

The genus *Novaculina* Benson, 1830 (Bivalvia: Pharidae: Pharellinae) represents a small group of peculiar freshwater bivalves with elongate shell living inside deep vertical burrows in substrata (Benson 1830; Nesemann et al. 2005; Liu and Zhang 1979). While other members of the Pharidae are exclusively marine taxa, *Novaculina* was considered a secondary freshwater clade (Annandale 1922; Nesemann et al. 2011). Recently, this hypothesis was supported on the basis of multi-locus phylogenetic reconstructions (Bolotov et al. 2018b).

The genus *Novaculina* contains four species with strictly allopatric ranges (Bolotov et al. 2018a). *Novaculina gangetica* Benson, 1830 was known to occur in the Ganges Basin in India and Bangladesh (Benson 1830; Subba Rao 1989; Khan et al. 2007; Baki et al. 2016) but was recently discovered in coastal basins of western Myanmar (Bolotov et al. 2018b). The range of *Novaculina siamensis* Morlet, 1889 covers the Bang Pakong and Pa Sak River basins in Thailand, and the Mekong Delta in Vietnam (Morlet 1889; Brandt 1974; Sayenko et al. 2017; Bolotov et al. 2018a). *Novaculina chinensis* Liu & Zhang, 1979 was described from the Yangtze Basin in China, and is abundant in benthic assemblages of large lakes such as Taihu (Liu and Zhang 1979; Qin 2008; He and Zhuang 2013; Ji et al. 2015; Hu et al. 2016). Finally, *Novaculina myanmarensis* Bolotov et al., 2018 was discovered in the Donthami and Ayeyarwady rivers in Myanmar (Bolotov et al. 2018a). The latter species was overlooked during a long-term period, although the presence of a *Novaculina* species (as *N. gangetica*) in the Ayeyarwady Delta was noticed at the end of 19th century (Theobald 1877).

This study aims to (1) reconstruct phylogeographic patterns for *Novaculina myanmarensis* and *N. gangetica* populations from Myanmar, (2) clarify the ranges of these species based on new occurrences and DNA barcoding data, and (3) discuss the taxonomic placement of two doubtful nominal taxa historically described within the genus *Novaculina*.

Material and methods

Altogether 23 sequences of the *cytochrome c oxidase subunit I* (*COI*) gene fragment for *Novaculina myanmarensis* (*N* = 15) and *N. gangetica* (*N* = 8) were used in this study (Table 1), including seven new sequences and 16 sequences from our earlier works (Bolotov et al. 2018a, 2018b). The DNA extraction, PCR, and sequencing of new samples followed protocols described previously (Bolotov et al. 2018a, 2018b). To study the phylogeographic affinities of Myanmar samples, we applied a median joining network approach using Network v. 4.6.1.3 software with default settings (Bandelt et al. 1999).

New localities of *Novaculina* spp. were found under our fieldwork in Myanmar in 2018-2020 (Table 2). Additionally, a body of available literature and museum collection data were compiled. Museum abbreviations are as follows: CAS California Academy of Sciences, San Francisco, United States of America; FFI Fauna & Flora International – Myanmar Program, Yangon, Myanmar; MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, United States of America; MUMNH Mahidol University Museum of Natural History, Nakhon Pathom, Thailand; RMBH Russian Museum of Biodiversity Hotspots, N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences, Arkhangelsk, Russia; and UMZC University Museum of Zoology, Cambridge, United Kingdom.

The updated map of *Novaculina* occurrences (Fig. 1) was compiled with ESRI ArcGIS 10 software (www.esri.com/arcgis). The topographic base of the map was created using free open sources such as Natural Earth Free Vector and Raster Map Data (www.naturalearthdata.com) and Global Self-consistent Hierarchical High-resolution Geography, GSHHG (http://www.soest.hawaii.edu/wessel/gshhg).

Results and discussion

Ranges of *Novaculina* spp. and biogeographic issues

New occurrences of *Novaculina* species presented in this study expand our knowledge on the distribution of several species (Fig. 1 and Tables 1-2). Here, we show that the range of *Novaculina myanmarensis* extends eastward to the Ataran River basin, another tributary of the massive Salween Estuary. Furthermore, new
occurrences from the Lower Ayeyarwady extend its range in this large freshwater system and support the historical report of Theobald (1877) on records of a *Novaculina* species in the Ayeyarwady Delta. In its turn, *Novaculina gangetica* was found to occur in the Dalet River, approximately 80 km SE from the previously known localities in the Kaladan – Lemro Basin, western Myanmar (Bolotov et al. 2018a, 2018b).

**Table 1.** List of *Novaculina* (Bivalvia: Pharidae) COI sequences used in this study.

| Species          | Locality                        | Freshwater basin | Sample ID | COI sequence | Reference              |
|------------------|---------------------------------|------------------|-----------|--------------|------------------------|
| *N. myanmarensis*| Myanmar: Winyaw River           | Ataran           | RMBH      | biv1030_1    | MW549329 This study    |
|                  | Myanmar: Winyaw River           | Ataran           | RMBH      | biv1030_2    | MW549330 This study    |
|                  | Myanmar: downstream of the Ayeyarwady River | Ayeyarwady | RMBH biv1014 |              | MW549326 This study    |
|                  | Myanmar: downstream of the Hlaing River | Ayeyarwady | RMBH biv1015_1 |              | MW549327 This study    |
|                  | Myanmar: downstream of the Hlaing River | Ayeyarwady | RMBH biv1015_2 |              | MW549328 This study    |
|                  | Myanmar: Donthami River         | Donthami         | RMBH biv0369_1 |              | MH670876 Bototov et al. (2018a) |
|                  | Myanmar: Donthami River         | Donthami         | RMBH biv0369_2 |              | MH670877 Bototov et al. (2018a) |
|                  | Myanmar: Donthami River         | Donthami         | RMBH biv0369_3 |              | MH670878 Bototov et al. (2018a) |
|                  | Myanmar: Donthami River         | Donthami         | RMBH biv0369_4 |              | MH670879 Bototov et al. (2018a) |
|                  | Myanmar: Donthami River         | Donthami         | RMBH biv0369_5 |              | MH670880 Bototov et al. (2018a) |
|                  | Myanmar: Ayeyarwady River       | Ayeyarwady       | RMBH biv0420_1 |              | MH670881 Bototov et al. (2018a) |
|                  | Myanmar: Ayeyarwady River       | Ayeyarwady       | RMBH biv0420_3 |              | MH670882 Bototov et al. (2018a) |
|                  | Myanmar: Ayeyarwady River       | Ayeyarwady       | RMBH biv0420_4 |              | MH670883 Bototov et al. (2018a) |
|                  | Myanmar: Ayeyarwady River       | Ayeyarwady       | RMBH biv0420_5 |              | MH670884 Bototov et al. (2018a) |
|                  | Myanmar: Ayeyarwady River       | Ayeyarwady       | RMBH biv0420_6 |              | MH670885 Bototov et al. (2018a) |
| *N. gangetica*   | Myanmar: Dalet River            | Dalet            | RMBH      | biv0661_2    | MW549324 This study    |
|                  | Myanmar: Dalet River            | Dalet            | RMBH      | biv0661_1    | MW549325 This study    |
|                  | Myanmar: Lemro River            | Lemro            | RMBH      | biv0150_1    | MF958986 Bototov et al. (2018b) |
|                  | Myanmar: Lemro River            | Lemro            | RMBH      | biv0150_2    | MF958987 Bototov et al. (2018b) |
|                  | Myanmar: Lemro River            | Lemro            | RMBH      | biv0150_3    | MF958988 Bototov et al. (2018b) |
|                  | Myanmar: Kaladan River          | Kaladan          | RMBH      | biv0151_1    | MF958989 Bototov et al. (2018b) |
|                  | Myanmar: Kaladan River          | Kaladan          | RMBH      | biv0151_2    | MF958990 Bototov et al. (2018b) |
|                  | Myanmar: Kaladan River          | Kaladan          | RMBH      | biv0151_3    | MF958991 Bototov et al. (2018b) |
Ng et al. (2020) recently discovered a population of *Novaculina siamensis* in the Tonle Sap River (Cambodia). Thus, this species occurs not only in the Mekong Delta and coastal rivers of the Gulf of Thailand (Morlet 1889; Brandt 1974; Sayenko et al. 2017; Bolotov et al. 2018a) but also in the Lower Mekong as far upstream as the Tonle Sap (approximately 300 km away from the coast).

The habitats of *Novaculina myanmarensis* we have recorded (Fig. 2) align with those described in earlier works on this species (Bolotov et al. 2018a). The collecting localities represent freshwater downstream sections of large and medium-sized rivers with clay bottom (Fig. 2A-B) and a large oxbow lake in the downstream of Ayeyarwady River (Fig. 2C). *Novaculina gangetica* is known to occur in similar environments (Bolotov et al. 2018a, 2018b). Ng et al. (2020) also collected *Novaculina siamensis* from cylindrical holes in clay bottom of the Tonle Sap River.

The network analyses reveal that *Novaculina gangetica* shares six COI haplotypes, two of which are common between different rivers (i.e. Kaladan + Lemro and Kaladan + Dalet) (Fig. 3A). The haplotypes are separated by one or two nucleotide substitutions only. Such a weak phylogeographic pattern may reflect relatively recent (Late Pleistocene) colonization of coastal rivers in Myanmar from the Ganges Basin but the DNA sequences of *Novaculina gangetica* from India and Bangladesh are not available.

Conversely, *Novaculina myanmarensis* shares clear phylogeographic structure with five COI haplotypes in rivers emptying to the Salween Estuary (Donthami and Ataran) and one unique COI haplotype in the Ayeyarwady Basin (Fig. 3B). This pattern could indicate that the species has evolved somewhere in rivers of the Salween Estuary, with a subsequent immigration into the Ayeyarwady Basin via a (sub)recent dispersal event. A shallow divergence (single nucleotide substitution) between the COI haplotypes from Ayeyarwady and Salween basins could indicate that this dispersal event took place in the Late Pleistocene, when the sea level decreased greatly, allowing connections between downstream sections of rivers (Voris 2000).
Table 2. Occurrences of *Novaculina* species (Bivalvia: Pharidae).

| Species            | Locality                                                                 | Latitude | Longitude | Reference                      |
|--------------------|---------------------------------------------------------------------------|----------|-----------|--------------------------------|
| *N. myanmarensis*  | Myanmar: Winyaw River near Myaing Kone village, Ataran River basin [sample ID: RMBH biv1030] | 15.9059  | 97.9874   | This study                     |
|                    | Myanmar: downstream of the downstream of the Hlaing River, Ayeyarwady Basin [sample ID: RMBH biv1015] | 17.7415  | 95.6265   | This study                     |
|                    | Myanmar: downstream of Donthami River [sample ID: RMBH biv0420]*            | 16.6935  | 97.5819   | Bolotov et al. (2018a)         |
|                    | Myanmar: Ayeyarwady River, Pakokku Region, near Thin Baw Kone village [sample ID: RMBH biv0369] | 17.6844  | 95.4731   | Bolotov et al. (2018a)         |
|                    | Myanmar: downstream of Donthami River [sample ID: RMBH biv0369]             | 14.2166  | 93.8359   | Bolotov et al. (2018b)         |
|                    | Myanmar: Ayeyarwady River, Pakokku Region, near Thin Baw Kone village [sample ID: RMBH biv1014] | 21.3146  | 95.0591   | Bolotov et al. (2018a)         |
|                    | Myanmar: Ayeyarwady River, Pakokku Region, near Thin Baw Kone village [sample ID: RMBH biv0369] | 21.2066  | 94.9062   | Bolotov et al. (2018a)         |
| *N. myanmarensis*  | Myanmar: downstream of Donthami River [sample ID: RMBH biv0420]*            | 16.6935  | 97.5819   | Bolotov et al. (2018a)         |
|                    | Myanmar: Ayeyarwady River, Pakokku Region, near Thin Baw Kone village [sample ID: RMBH biv1014] | 21.3146  | 95.0591   | Bolotov et al. (2018a)         |
|                    | Myanmar: downstream of Donthami River [sample ID: RMBH biv0369]             | 14.2166  | 93.8359   | Bolotov et al. (2018b)         |
| *N. gangetica*     | Myanmar: Dalet River near Thaphanbin village [sample ID: RMBH biv0661]       | 19.9939  | 93.8359   | This study                     |
|                    | Myanmar: Lemro River [sample ID: RMBH biv150]                               | 20.6150  | 93.2481   | Bolotov et al. (2018b)         |
|                    | India: Ganges River at Vindhyachal upstream of Mirzapur                      | 25.1666  | 82.5072   | Nesemann et al. (2005)         |
|                    | India: Hooghly River, downstream of Howra                                   | 22.4278  | 88.1368   | Nesemann et al. (2005)         |
|                    | India: Ganges River at Varanasi                                             | 25.3279  | 83.0464   | Subba Rao (1989)               |
|                    | India: Ganges River at Patna                                                | 25.6589  | 85.1573   | Nesemann et al. (2011)         |
|                    | India: Calcutta [Sample IDs: MCZ 224805 and UMZC 1.101225]*                | 22.6000  | 88.3000   | Bolotov et al. (2018a)         |
| *N. gangetica*     | Bangladesh: Turag River at Tangi Bridge                                     | 23.8997  | 90.4081   | Baki et al. (2016)             |
| *N. gangetica*     | Bangladesh: Muyur River                                                     | 22.7719  | 89.5402   | Khan et al. (2007)             |
| **N. siamensis**   | Cambodia: Tonle Sap River in Kaoh Thkov, Chol Kiri District, Kampong Chhnang Province [Sample ID: MUMNH PHA.001] | 12.0588  | 104.7729  | Ng et al. (2020)               |
|                    | Cambodia: Tonle Sap River in Samrethti Chey, Kampong Tralach district, Kampong Chhnang Province [Sample ID: MUMNH PHA.003] | 11.8987  | 104.7671  | Ng et al. (2020)               |
|                    | Thailand: Chantakam [Bang Pakong River basin]*                               | 14.0000  | 102.0000  | Morlet (1889)                  |
| *N. siamensis*     | Thailand: Pa Sak River near Saraburi                                        | 14.5304  | 100.9113  | Brandt (1974)                  |
|                    | Vietnam: Ba Lai River, Mekong Delta                                         | 10.2647  | 106.4397  | Sayenko et al. (2017)          |
| *N. chinensis*     | China: Lake Taihu, Wuxi*                                                    | 31.4402  | 120.3143  | Liu and Zhang (1979); Qiu (2008) |
|                    | China: Lake Taihu, southwest                                                | 31.1843  | 120.4267  | Ji et al. (2015)               |
| *N. chinensis*     | China: Lake Hongze                                                          | 33.3075  | 118.7100  | Hu et al. (2016)               |
| *N. chinensis*     | China: Lake Chaohu                                                          | 31.5224  | 117.5616  | Cai et al. (2012)              |
| *N. chinensis*     | China: Yintan                                                              | 28.0333  | 117.0667  | Wen and Zhu (1999)             |

*Type localities of the corresponding taxa.
Figure 2. Habitats of Novaculina myanmarensis in Myanmar (new occurrences). (A) Winyaw River, Ataran Basin [sample ID: RMBH biv1030]. (B) Downstream of the Hlaing River, Ayeyarwady Basin [sample ID: RMBH biv1015]. (C) Large oxbow lake, downstream of the Ayeyarwady River [sample ID: RMBH biv1014]. (Photos: Than Win [A] and Ilya V. Vikhrev [B-C])

Taxonomic remarks on doubtful nominal taxa described as Novaculina representatives

Novaculina gangetica theobaldi Hanley & Theobald, 1874
=Novaculina gangetica? var. theobaldi Hanley & Theobald (1874): 48, pl. 116, fig. 10.

Type: Location unknown.

Type locality: Tenasserim River, Pegu [Tanintharyi River, Myanmar].

Proposed taxonomic placement: a junior synonym of Cultellus maximus (Gmelin, 1791) (Bivalvia: Pharidae).

Comments: It is a somewhat enigmatic taxon. Hanley and Theobald (1874: 48) introduced it as follows: “This was regarded by Benson as a large variety of his Gangetic species: it looks distinct but without more specimens its separation would, perchance, be unadvisable”. The shell of this clam was illustrated in scale (Hanley and Theobald 1874: pl. 116, fig. 10). This shell is exceptionally large compared with that of Novaculina gangetica presented on the same plate (Hanley and Theobald 1874: pl. 116, fig. 7). Based on the mean size of the latter species, the illustrated shell of Novaculina gangetica theobaldi is at least 12-15 cm in length. Large size and a slightly concave ventral margin of the shell clearly indicate that it is not a Novaculina species but a representative of larger estuarine razor clams. There is the only one razor clam
species in Myanmar having similar shell habitus and such a large size, i.e. *Culpellus maximus*. Hence, we tentatively assign the nominal taxon *Novaculina gangetica theobaldi* to this estuarine species.

![Figure 3](image-url) - Median joining networks of *Novaculina* spp. based on the COI gene fragment. (A) *N. gangetica* (*N* = 8). (B) *N. myanmarensis* (*N* = 15). The circle size is proportional to the number of available sequences belonging to the given haplotype (the smallest = 1). The red numbers near branches indicate the number of nucleotide substitutions between haplotypes. The color filling indicate river drainage basins.

**Novaculina andamanensis** Preston, 1908

≡*Novaculina andamanensis* Preston (1908): 209, pl. 16, fig. 40.
≡*Novaculina andamanensis* Subba Rao (1989): 223, figs 635, 636.
≡*Azorinus emerginata* [sic!] Ramakrishna et al. (2004): 49.
≡*Azorinus emarginata* Ramakrishna & Dey (2010): 220.
≡*Azorinus coarctatus* Bolotov et al. (2018): 9.

Type: Holotype ZSI M4060/1 [by monotypy]; Zoological Survey of India, Kolkata, India. Subba Rao (1989) illustrated this specimen as the holotype. Later, Ramakrishna et al. (2004) assigned ZSI M4060/1 to be the holotype, and considered another specimen (ZSI M20765/4) as a paratype. However, the protologue contained the description and measurements of a single shell (Preston 1908). Hence, the paratype status of the specimen ZSI M20765/4 is rather doubtful and requires future confirmation.

Type locality: Andaman Islands.

Proposed taxonomic placement: a junior synonym of *Azorinus coarctatus* (Gmelin, 1791) (Bivalvia: Solecurtidae).

Comments: This species was described as follows: “Shell oblong, elongate, inequilateral, constricted towards the middle, pure white, bearing traces of having been covered with a yellowish brown periostracum, concentrically striate; dorsal margin slightly sloped anteriorly; ventral margin excavated in the middle, anterior side rounded; posterior side produced, somewhat angled below; umboes small” (Preston 1908: 209). Subba Rao (1989) noted that the validity of this species is doubtful but listed it in the original combination. Based on the protologue, this nominal taxon shares a concave ventral margin and shell with concentric striations that weakly corresponds to a *Novaculina* species. Ramakrishna et al. (2004) considered this nominal taxon as a synonym of *Azorinus emarginata* (Spengler, 1794) [= *A. chamasolen* (da Costa, 1778)]. However, it most likely belongs to *Azorinus coarctatus*, as it was suggested earlier based on morphological features such as somewhat trapezoidal shell with concave ventral margin (Bolotov et al. 2018a).
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