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RESEARCH ARTICLE

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A new genus and two new, rare freshwater mussel (Bivalvia: Unionidae) species endemic to Borneo are threatened by ongoing habitat destruction

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Abstract

1. Most of the Bornean endemic freshwater mussel (Unionida) species known to date have not been recorded by science for the past 50 years or more, owing to a lack of research effort and presumed population losses.
2. This study assessed current patterns and recent changes in the diversity and distribution of freshwater mussels in north-eastern Borneo. Physical surveys and interviews were conducted at 24 sites, and anecdotal evidence for current or historical presence of mussels was collected for a further 13 sites.
3. Native species, i.e. *Schepmania* sp. and *Khairuloconcha sahanae* gen. & sp. nov., were only found in one small stream of the Kinabatangan River basin within the Gomantong Forest Reserve, whereas the non-native *Sinanodonta* cf. *woodiana* was common across the study area.
4. Molecular phylogenetics (five genes) of the native taxa, including comparative material from West Kalimantan and Sarawak, revealed: (i) the presence of a new genus with two new, rare species: *Khairuloconcha lunbawangorum* sp. nov. in the Limbang River basin and *K. sahanae* in the Kinabatangan River basin; (ii) that *Khairuloconcha* and *Ctenodesma* form the Bornean endemic tribe Ctenodesmini trib. nov.; and (iii) that *Schepmania* represents another Bornean endemic tribe Schepmaniini trib. nov.
5. Both *Khairuloconcha* gen. nov. species are known from a single stream each and are apparently restricted to forest stream habitats where they occur at very low densities. *Schepmania* appears to have a severely contracted range in the Kinabatangan and adjacent basins. We urgently call for full protection of the currently known sites of *K. lunbawangorum* and *K. sahanae*, and development of an action plan to save the Bornean freshwater mussel fauna.

KEYWORDS

biodiversity, Borneo, conservation, endemic species, freshwater mussels, invertebrates, phylogeny, *Sinanodonta woodiana*, Unionida

1 | INTRODUCTION

Borneo exhibits an exceptionally high rate of endemism of freshwater mussels (Bivalvia: Unionida), with 13 of the 18 currently recognized native species being restricted to this island, all of which belong to the family Unionidae (see Table 1 in Zieritz et al., 2020b). However, most of these species have not been recorded for several decades, and their taxonomy is based mostly on shell morphology as DNA sequence data are lacking (Figure 1a). The 13 Bornean endemic freshwater mussel species recognized at present are primarily known from specimens collected in the 19th and early 20th century. Only a few records (<15) of Bornean freshwater mussels have been reported in the second half of the 20th century (Graf & Cummings, 2021a), including four records from Sabah (northern Borneo) collected in 1962–1964 and identified as *Ctenodesma borneensis* (Issel, 1874) (FMNH 116932 (FMNH = Field Museum of Natural History, Chicago, USA)), *Schepmania niewenhuisi* (Schepman, 1898) (FMNH 116933, FMNH 118893) and *Schepmania parcesculpta* (Martens, 1903) (USNM 656126 (USNM = National Museum of Natural History, Washington, USA)).

The first DNA sequence data of Bornean freshwater mussels was generated in 2016, when our team commenced a series of targeted expeditions across northern Borneo, comprising the Malaysian states of Sarawak and Sabah, and Brunei (Figure 1a) (Gallardo et al., 2018; Zieritz et al., 2018c; Zieritz et al., 2020b). This work showed that, with the exception of the relatively common species *Rectidens sumatrensis* (Dunker, 1852), all native (and particularly endemic) species appear to be rare and, in some cases, may already be extirpated. Out of 115 sites surveyed between 2016 and 2018, endemic Bornean mussels were found only at a single site in a small stream within a patch of intact rainforest (Zieritz et al., 2020b). That population, of which only three individuals were found, was identified as *C. borneensis* based on the species' small size, elongated shell shape, yellowish-brown epidermis with green rays and fine sculpture on the shell disc, and morphological comparison with the type specimen of *Unio plicatulus* Lea, 1859 (Figure 2).

Owing to the paucity of data, the reasons for the declines of native Bornean freshwater mussels are not well understood. However, there is little doubt that the industrial-scale deforestation and land-use change from primary dipterocarp forest to secondary forest and, ultimately, to agricultural monocultures (now predominantly oil palm) since the 1960s has been a major driver of freshwater mussel population losses on the island (Bryan et al., 2013; Gallardo et al., 2018). These practices result in high levels of soil erosion, strongly increasing sediment yield, and organic and inorganic pollution (via agricultural run-off) of rivers (Figures 3b and d) (Douglas, 1996; Igwe & Onyegbado, 2007; Rulli et al., 2019), all of which adversely affects freshwater mussels directly by degrading habitat quality or indirectly by reducing host fish populations that they require to complete their life cycles (Wächtler, Mansur & Richter, 2001; Wilkinson et al., 2018; Zieritz et al., 2018b). Other potential drivers of declines in Borneo's freshwater mussel populations include pollution from domestic and industrial sewage, hydrological alterations, mining, climate change and invasive species (Dudgeon et al., 2006; Zieritz et al., 2018b; Sundar et al., 2020).

Whereas native mussel species have declined on the island, humans have repeatedly introduced and are actively spreading the non-native *Sinanodonta* cf. *woodiana* (Lea, 1834) for food and ornamental purposes (Zieritz et al., 2018c). A native to the Yangtze River basin, *S.* cf. *woodiana* was first reported in Borneo from a market in Sabah (Bogan & Schilthuizen, 2004) and is now the most common and widespread unionid species in Borneo, particularly in Sabah (Figure 1a). In 2018, another non-native species, *Sinanodonta lauta* (Martens, 1877), native to Japan, was recorded for the first time in Borneo from a pond in the Lawas district (Zieritz et al., 2020b). These non-native species may exacerbate the damaging effects of anthropogenic habitat degradation on native species as a result of interspecific competition and by inducing cross-resistance of host fish (Donrovich et al., 2017).

As highlighted by Zieritz et al. (2020b), more survey work is urgently needed to locate and subsequently to protect any remaining populations of native freshwater mussels in Borneo. Considering the vast area of virtually unsurveyed habitat (Figure 1a), the initial focus should therefore be put on regions with historical records of freshwater mussels. In Malaysian Borneo, this specifically includes the river basins of eastern Sabah, including the Kinabatangan River (Figure 1). In Indonesian Borneo (i.e. Kalimantan), where no DNA sequence data of freshwater mussels are available to date, historical records are particularly concentrated in the Kapuas River in West Kalimantan, the Mahakam River in East Kalimantan, and the river basins of South Kalimantan (including the Barito; Figure 1a). These surveys should also involve gathering data on past occurrences of freshwater mussel populations, as the data are crucial for determining recent changes in species diversity and distribution ranges. Although data availability in the published literature and museum records are often insufficient in this respect, local ecological knowledge can provide an alternative source of this information, especially in Southeast Asia (Silvano & Valbo-Jørgensen, 2008; Zieritz et al., 2018c; Zieritz et al., 2020b), where freshwater mussels are widely being used as a source of food and material (Zieritz et al., 2018a).

The present study aimed to assess current patterns and recent changes in the diversity and distribution of freshwater mussels in north-eastern Borneo, focusing on the Kinabatangan River basin, through field surveys and interviews. In addition, comparative material from West Kalimantan and Sarawak is also discussed, which was collected in the course of the continuing, greater effort towards unravelling these patterns across the whole of Borneo. Molecular phylogenetic analyses (five genes) of sampled individuals identified several previously undescribed lineages. Two new tribes are described, i.e. Ctenodesmini trib. nov. and Schepmaniini trib. nov., as well as a new genus (*Khairuloconcha* gen. nov.) and two new species (*Khairuloconcha lunbawangorum* sp. nov. and *Khairuloconcha sahanae* sp. nov.), both of which are endemic to Borneo, with each known from only a single stream. Specific threats to these endemic mussel species are discussed, and actions towards their conservation and that of the Bornean freshwater mussel fauna in general are recommended.

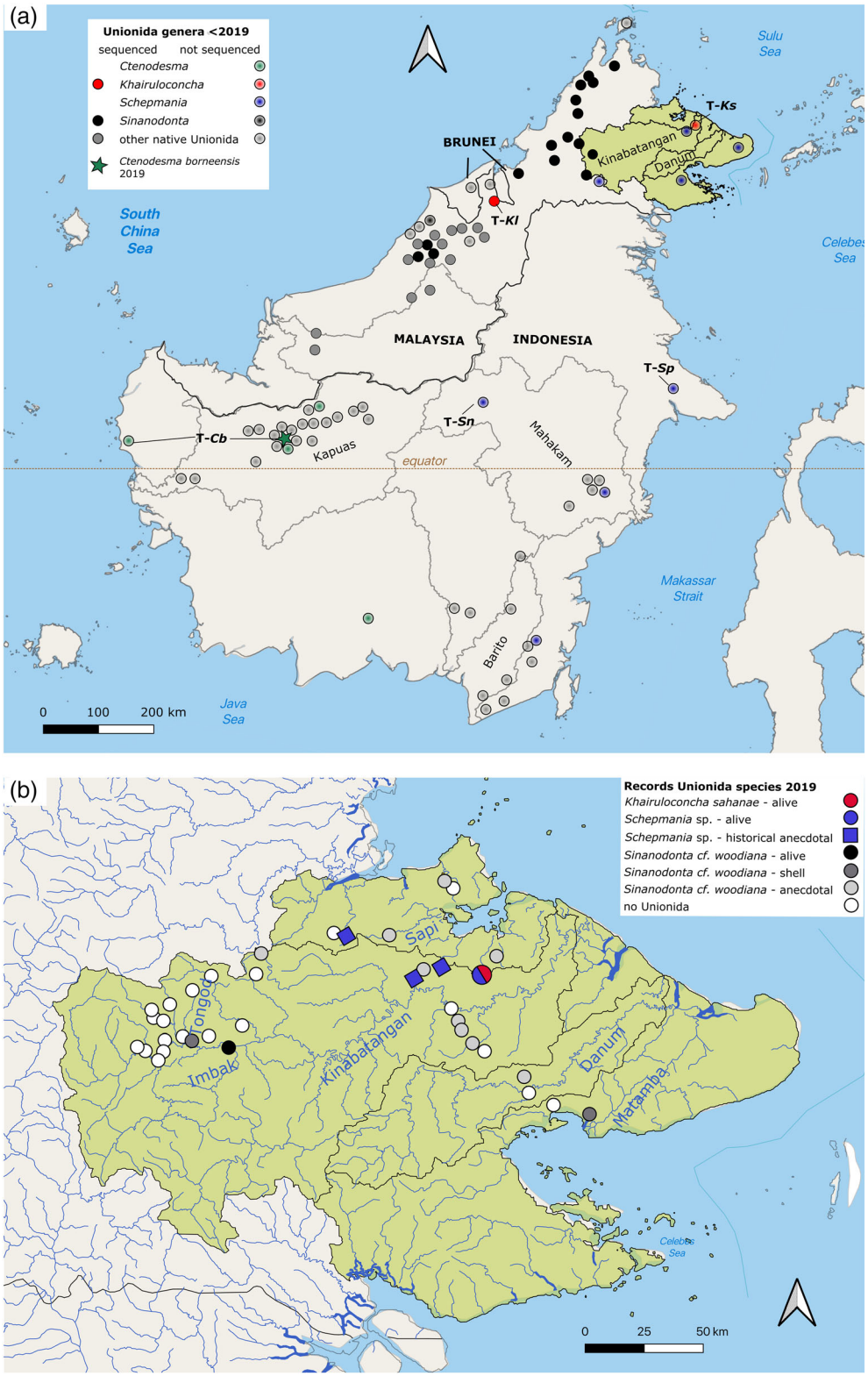

FIGURE 1 (a) Locations of freshwater mussel (Bivalvia: Unionida) genus-level records (pre-2019) in Borneo and locality of collection of *Ctenodesma borneensis* in Kapuas basin, Kalimantan (2019). Data collated from personal records, http://mussel-project.uwsp.edu and https://bioportal.naturalis.nl, including only records that were georeferencable at HydroBASINS level 4 (Lehner & Grill, 2013) or higher. (b) Locations of study sites and species-level records collected in Sabah in 2019. Green shading, level 6 HydroBASINS where surveys were conducted; grey outline, level 4 HydroBASINS outside of study area. Abbreviations: T-Cb, Type locality of *Ctenodesma borneensis*; T-Kl, Type locality of *Khairuloconcha lunbawangorum* sp. nov.; T-Ks, Type locality of *Khairuloconcha sahanae* sp. nov.; T-Sn, Type locality of *Schepmania niewenhuisi*; T-Sp, Type locality of *Schepmania parcesculpta*

2 | METHODS

2.1 | Study area

Fieldwork was conducted in eastern Sabah in the Kinabatangan and Danum River basins as well as the surrounding coastal basins (Figure 1). Study sites were situated within the freshwater ecoregions of Borneo highlands and north-eastern Borneo (Abell et al., 2008). Dominating geological units are ophiolitic and sedimentary rocks in the upper Kinabatangan and Danum catchments, and Miocene melanges and sedimentary rocks in the lower river catchments (Balaguru & Nichols, 2004). The area features several protected areas, including

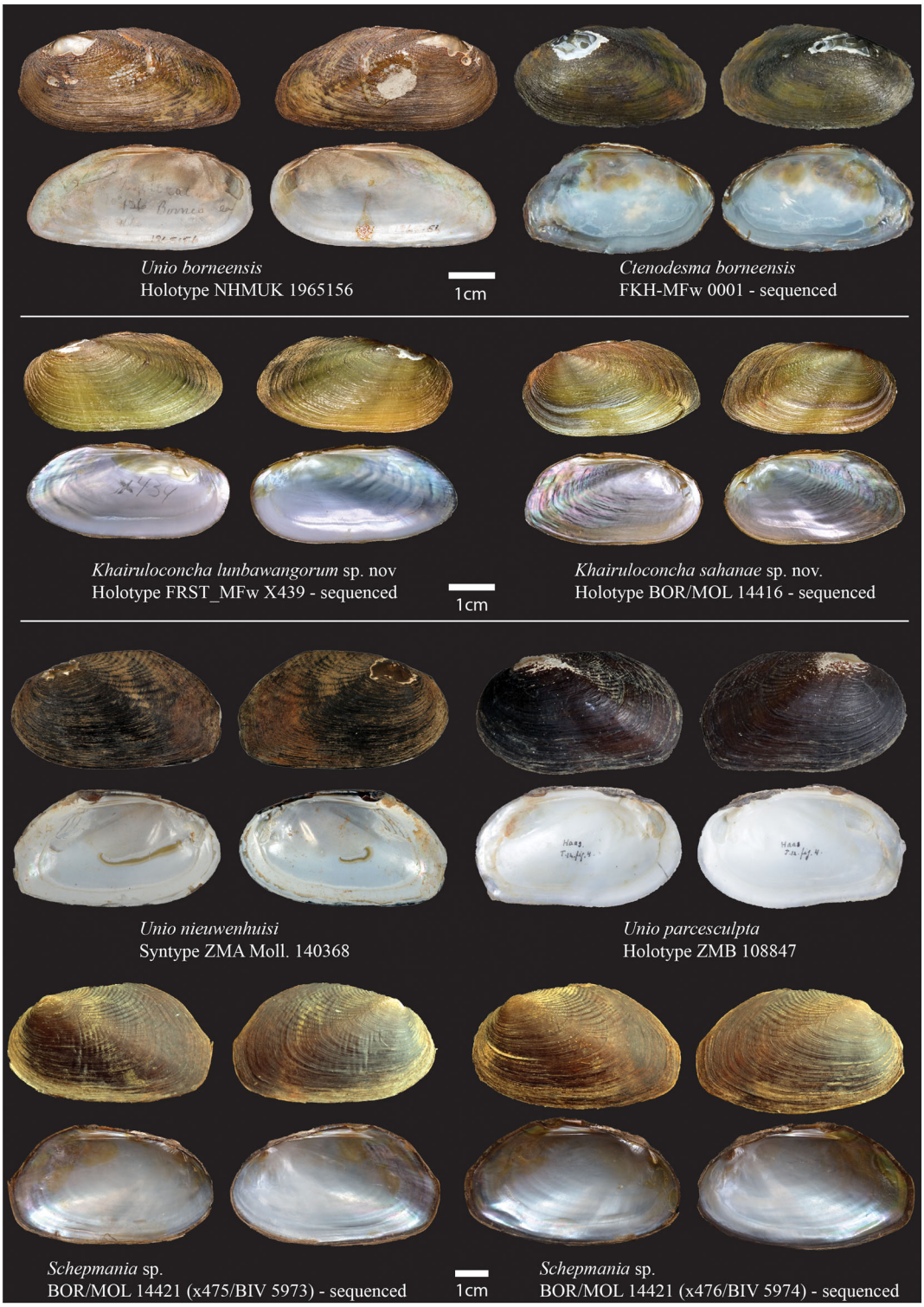

FIGURE 2 Type specimens and sequenced specimens of the treated Ctenodesmini trib. nov. and Schepmaniini trib. nov. taxa. Abbreviations: BOR, BORNEENSIS Collection, Universiti Malaysia Sabah, Malaysia; FKH, Fahutan Kapuas Hulu Collection, Tanjungpura University, Indonesia; FRST, Faculty of Resource Science & Technology Collection, Universiti Malaysia Sarawak, Malaysia; NHMUK, Natural History Museum, London, UK; ZMA, Zoölogisch Museum Amsterdam, Netherlands; ZMB, Museum für Naturkunde, Berlin, Germany

the Kinabatangan Wildlife Sanctuary (260 km^2), the Protection Forest Reserves of Gomantong (51 km^2) and Tawai (227 km^2), and the Virgin Jungle Reserve Kabili Sepilok (43 km^2; UNEP-WCMC & IUCN, 2014–2020). Although the region is renowned for its exceptional biodiversity and is a popular nature tourism destination, land-use conversion from the natural forest into commercial logging forest and later into oil palm

FIGURE 3 Photographs of sites in eastern Sabah where freshwater mussel occurrences were confirmed by physical surveys or interviews in May 2019. (a) Stream (Sungai Dayang) in Gomantong Forest Reserve, where *Schepmania* sp. and *Khairuloconcha sahanae* sp. nov. were collected alive; (b) tributary of River (Sungai) Imbak, where *Sinanodonta* cf. *woodiana* was collected alive; (c) River (Sungai) Tongod, where *S.* cf. *woodiana* shells were collected; (d) River (Sungai) Lokan, where *S.* cf. *woodiana* presence was confirmed anecdotally in interviews but could not be confirmed in physical surveys

plantation has reduced primary forest to narrow strips along the riparian corridor (Goh, 2017).

2.2 | Field surveys

Field surveys in Sabah were conducted from 9 to 16 May 2019, during the dry season when water levels are lowest and access to mussels is therefore optimal. A total of 32 sites were surveyed. Survey methodology followed that of Zieritz et al. (2020b). At each site, covering about 100–300 m river length, at least three local individuals were initially interviewed to ask about safe access to sampling sites, presence of estuarine crocodiles (*Crocodylus porosus*), and historical and current presence of mussels. Interviewees were shown photographs or, if available, shells of mussel genera known from Borneo and asked to identify any that used to be present or are still present at the site. Where access was safe (24 sites), environmental parameters known to affect tropical mussel distribution (Zieritz et al., 2016; Gallardo et al., 2018) were recorded: (i) temperature and (ii) pH readings were taken using a YSI ProDSS Water Quality Multiparameter probe. Water samples were taken with acid-washed, dried sampling bottles, and 300–500 ml filtered through a pre-weighed Whatman GF/F filter for analysis of: (iii) total suspended solids; (iv) nitrate (NO_3-N), (v) total ammoniacal nitrogen; and (vi) soluble reactive phosphorus (SRP) on the day of sampling (Eaton et al., 2005). Total suspended solids was calculated as the difference between the initial weight of the filter paper and after drying to constant weight at 105°C. Concentrations of NO_3-N, total ammoniacal nitrogen and SRP were determined from filtered water samples by the ascorbic acid, cadmium reduction and salicylate methods, respectively, using a calorimeter (Nutrient Auto Analyzer, HACH, DR900; HACH, 2012).

Mussel surveys were conducted by hand and net until genera identified by local people were found, or for at least one person-hour, following the same protocol as described in Zieritz et al. (2018c). Where mussels were found, voucher specimens and tissue snips were collected and preserved in absolute ethanol and deposited at the BORNEENSIS Collection, Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah (BOR/MOL; Supporting Information 1). Except for vouchers, all other specimens were returned to their habitat. Additional interviews were conducted on an ad-hoc basis at markets, homestays and a biological field centre.

On 25 August 2019, *Ctenodesma borneensis* were collected from its putative type locality 'north-western Borneo' ('Nordwestliches Borneo' in von Martens (1867) incorrectly translated to 'Nord-Est Borneo' by Issel (1874)), specifically from the Sungai (River) Seberuang

(alternative spellings: Sebruang, Sebroang), Kapuas River basin, West Kalimantan (Figure 1a). A voucher specimen (FKH-MFw0001) was deposited at the Fahutan Kapuas Hulu collection, Tanjungpura University, Pontianak, West Kalimantan, Indonesia (FKH; Supporting Information 1).

2.3 | Species identification, and morphological and phylogenetic analysis

Collected specimens were identified to species level through an integrative morphological–molecular approach. Genomic DNA was extracted from tissue samples of the newly collected and other selected available specimens (Supporting Information 1), using a standard high-salt protocol (Sambrook, Fritsch & Maniatis, 1989) or the Jetquick tissue DNA Spin Kit (Genomed) following the manufacturer's protocol. Female lineages of mitochondrial cytochrome c oxidase subunit 1 (COI) were amplified and sequenced in both directions from all extracts using primer pair LCO22me2 + HCO700dy2 (Walker et al., 2006; Walker et al., 2007). For native species, additional sequences were generated for the large ribosomal subunit rRNA 16S (16SL + 16SH; Palumbi et al., 1991); the mtDNA ND1 (Leu-uurF and LoGlyR; Serb, Buhay & Lydeard, 2003); the small ribosomal subunit rDNA 18S (18Sa2.0 + 9R; Giribet et al., 1996); and the large ribosomal subunit 28S (28S-RD1.3f and 28S-rD4b; Whiting, 2002). Polymerase chain reaction conditions followed Froufe et al. (2016) and Bolotov et al. (2016) for 18S, with annealing temperatures of 48 and 50°C (only ND1). As the selected primer pair failed to amplify the 16S fragment in *C. borneensis*, amplification using an alternative primer pair (primers 16SA + 16SB; Palumbi, 1996) was then attempted. Amplified DNA templates were purified and sequenced by the commercial company Macrogen using the same primers. Sequences were cleaned up in program MEGA X (Kumar et al., 2018) and deposited in Genbank (accession numbers in Supporting Information 1).

For COI barcoding and to identify the generic position of each sequenced individual, a preliminary COI alignment with all newly sequenced individuals and representatives from most previously published unionid genera was produced and analysed with a Bayesian Inference (BI) phylogenetic approach, using MrBayes 3.2.7a (Ronquist et al., 2012) with 20×10^6 generations sampled at intervals of 1,000 generations on a single partition with model GTR + I + G.

Five alignments corresponding to the sequenced markers were then constructed with the newly sequenced individuals and representatives from available taxa belonging to the four described tribes within the subfamily Gonideinae (Supporting Information 1). Sequences from species belonging to the unionid subfamily Ambleminae and the Margaritiferidae were included as an outgroup following the relationships recovered in Pfeiffer, Breinholt & Page (2019). Each marker dataset was aligned using the stand-alone version of GUIDANCE2 (Sela et al., 2015) with the MAFFT multiple sequence alignment algorithm (version 7; Katoh & Standley, 2013) using default parameters. As the 16S fragment of *C. borneensis* failed to amplify (see section 3), two datasets were assembled for phylogenetic analyses: (i) a concatenated COI + ND1 + 16S + 18S + 28S dataset coding 16S nucleotides of *C. borneensis* as 'missing data'; and (ii) a concatenated COI + ND1 + 18S + 28S dataset. The best-fit number of partitions and substitution models were then selected for BI with PartitionFinder2 using a greedy search approach, MrBayes model set and the Bayesian Information Criterion (Lanfear et al., 2017); and for maximum likelihood (ML) with ModelFinder (Kalyaanamoorthy et al., 2017). BI analyses implemented in MrBayes 3.2.7a (Ronquist et al., 2012) were initiated with program-generated trees and four Markov chains with default incremental heating. Two independent runs of 20×10^6 generations were sampled at intervals of 1,000 generations, producing a total of 20,000 trees. Burn-in was determined upon the convergence of loglikelihood and parameter values using Tracer 1.7.1 (Rambaut et al., 2018). ML analyses implemented in IQ-TREE 2.1.1 (Minh et al., 2020) were conducted with initial tree searches, followed by 10 independent runs and 10,000 ultrafast bootstrap replicates.

The genus- and species-level nomenclatural acts proposed here were registered at ZooBank under the Life Sciences Identifier – urn:lsid:zoobank.org:pub: C357B255-63D1-4F87-9F51-FB5B8B061235. This included material from the collection of the Faculty of Resource Science & Technology, Universiti Malaysia Sarawak (FRST).

3 | RESULTS

3.1 | Diversity and distribution

Full surveys were conducted at 24 sites (Figure 1b). Live specimens were found at two of these sites, while only shells were collected from another two sites. In addition, anecdotal evidence for current or historical presence of mussels was collected for a further 13 sites (Figure 1b).

Native species were found only at one site, in a small stream (locally referred to as Sungai Dayang) situated within the Gomantong Forest Reserve draining initially into the River Menanggul and ultimately, the lower Kinabatangan River (Figures 1b and 3a; personal communication R. Amandus, Gomantong Forest Reserve). The presence of mussels was confirmed initially by Forest Reserve staff, and numerous empty shells were found by us within the first 10 person-minutes of surveying. However, live specimens were found only after about 15 person-hours in a single dense aggregation at the stream edge in mud–sandy substrate underneath roots of bank vegetation (Figure 3a). Within about 20 person-minutes, 47 *Schepmania* sp. and 1 *K. sahanae* sp. nov. (see section 3.4 below for details) were collected. In addition, >80 shells of *Schepmania* sp. and five shells of *K. sahanae* were found. In comparison with other study sites, conditions at this site were characterized by colder water temperature (26.3°C *vs*. an average of 30.4°C and 29.5°C at sites with *S.* cf. *woodiana* and without unionids, respectively), low pH (6.8 *vs*. 7.3

and 7.1), and high concentrations of NO_3-N (0.04 mg L^{-1} *vs*. 0.02 and 0.01) and SRP (0.49 mg L^{-1} *vs*. 0.21 and 0.19; Figure 4).

No live specimens, shells or anecdotal evidence of the current presence of native mussel species were found at any other study site, but anecdotal evidence for the historical presence of *Schepmania* sp. was collected from three independent sources (Figure 1b): (i) a female vendor (age ~60 years) selling freshwater shellfish at Beluran town market stated that several decades ago, *Schepmania* sp. used to be present in small, sandy streams near 'Kampung Kepod, Batu 54', situated in the drainage of the coastal River Sapi (Figure 1b), but has since disappeared; (ii) a female vendor (age ~40 years) selling fish at Kinabatangan market stated that *Schepmania* sp. used to be present in some of the small tributaries of the Kinabatangan in this area, but disappeared several decades ago; (iii) the owner of a small homestay south of the town of Kinabatangan (male, age ~50 years) also stated that *Schepmania* sp. used to be present in this area, but has not been seen for several decades.

Live specimens of *Sinanodonta* cf. *woodiana* were collected in a small tributary of Sungai Imbak, situated within an oil palm plantation in the upper Kinabatangan catchment (Figures 1b and 3b). Densities were moderate, and seven specimens were collected within approximately one person-hour. Shells of this species were found in Sungai Tongod, also in the upper Kinabatangan catchment, and in the coastal Sungai Matamba basin near the city of Lahad Datu (Figures 1b and 3c). Anecdotal records of current *S.* cf. *woodiana* presence were also collected from other tributaries of the upper, middle and lower Kinabatangan, the Danum river basin, and across coastal river basins, i.e. Sungai Sendala, Sungai Segaliud and Sungai Suanlamba, which could not be surveyed owing to the presence of crocodiles (Figures 1b and 3d).

3.2 | COI barcoding

The newly sampled specimens from eastern Sabah belonged to three different species, and the initial COI-BI tree positioned all except *Sinanodonta* cf. *woodiana* within the Gonideinae. The *Sinanodonta* cf. *woodiana* sequence was 100% identical to that of specimens x284, x289, x294, x354, x363 and x372 (Genbank accession numbers MG591509–11, MG591516–17, MG591519) originating from other river basins of Sabah and Sarawak, i.e. Sungai Wariu, Sungai Bongan and Sungai Suai. COI sequences of the

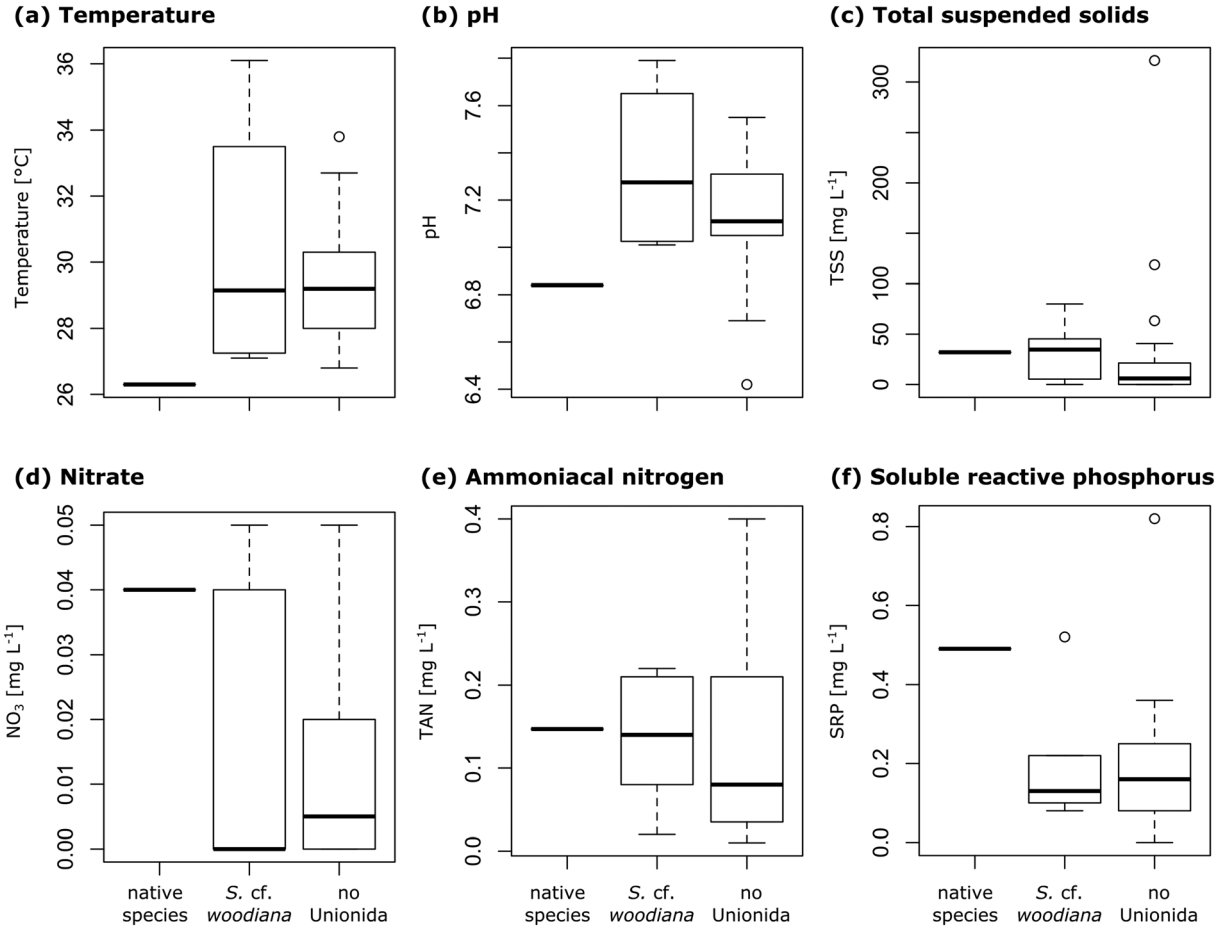

FIGURE 4 Variation in water quality parameters in May 2019 across 24 study sites in eastern Sabah with present occurrence of native freshwater mussel species *Khairuloconcha sahanae* sp. nov. and *Schepmania* sp. (one site), non-native *Sinanodonta* cf. *woodiana* (five sites), and no Unionida (18 sites)

remaining species were highly divergent from available sequences in Genbank, with the closest matches being members of the Gonideinae, i.e. *Gonidea angulata* (e.g. MN957829) for *Schepmania* sp. with 84.1% similarity, and '*Ctenodesma borneensis*' (=*Khairuloconcha lunbawangorum*; MN900788–90) for *Khairuloconcha sahanae* with 93.7%. The best matches for *Ctenodesma borneensis* collected from the type locality in the Kapuas River basin were *Hyriopsis bialata* (MG025690) and *Contradens* (=*Lens*; Pfeiffer et al., 2021) sp. (KX865925) with 87.9% similarity, respectively.

3.3 | Phylogenetic position of Bornean endemic species

Both of the primer pairs applied failed to amplify the 16S fragment of *C. borneensis*. Topologies of ML and BI trees were identical for concatenated COI + ND1 + 16S + 18S + 28S and COI + ND1 + 18S + 28S datasets, respectively. Topologies of trees for concatenated COI + ND1 + 16S + 18S + 28S and COI + ND1 + 18S + 28S datasets were identical with respect to the positions of the Bornean endemic species (Figure 5 and Supporting Information 2). The two *Khairuloconcha* species were recovered as sister to *Ctenodesma borneensis*, with strong nodal support (PP/UF = 0.99/91 and 0.92/88 for COI + ND1 + 16S + 18S + 28S and COI + ND1 + 18S + 28S, respectively), together forming the Bornean endemic tribe Ctenodesmini trib. nov. The Ctenodesmini were in turn consistently recovered as sister to the Contradentini + Rectidentini again with strong nodal support. COI uncorrected *p*-distances were 6.47% between *K. lunbawangorum* and *K. sahanae*, 13.25% between *C. borneensis* and *K. lunbawangorum*, and 13.71% between *C. borneensis* and *K. sahanae*, respectively.

The two sequenced *Schepmania* sp. specimens exhibited identical sequences and were consistently recovered as a previously unrecognised and divergent sister-group to the Pseudodontini that is described here as the tribe Schepmaniini trib. nov..

3.4 | Taxonomy

Family Unionidae Rafinesque, 1820

Subfamily Gonideinae Ortmann, 1916

Tribe Schepmaniini trib. nov. Lopes-Lima, Pfeiffer & Zieritz

Type Genus: *Schepmania* Haas, 1910.

Diagnosis: The Schepmaniini is distinguished from all other Gonideinae taxa in Southeast Asia (Chamberlainiini, Contradentini, Ctenodesmini, Pseudodontini, Rectidentini) by its ovate shell outline, the presence of a strongly sculptured posterior slope and largely smooth shell disk, robust pseudocardinal and lateral teeth, and an obvious ligamental fossette.

Distribution: Eastern Borneo.

Genera:

Schepmania Haas, 1910

Remarks: The higher-level classification of *Schepmania* has varied substantially over the past 50 years, having been placed in the Margaritiferidae (Starobogatov, 1970; Bogatov, Prozorova & Starobogatov, 2003), Unionidae *incertae sedis* (Graf & Cummings, 2007; Lopes-Lima et al., 2017; Zieritz et al., 2018b), and

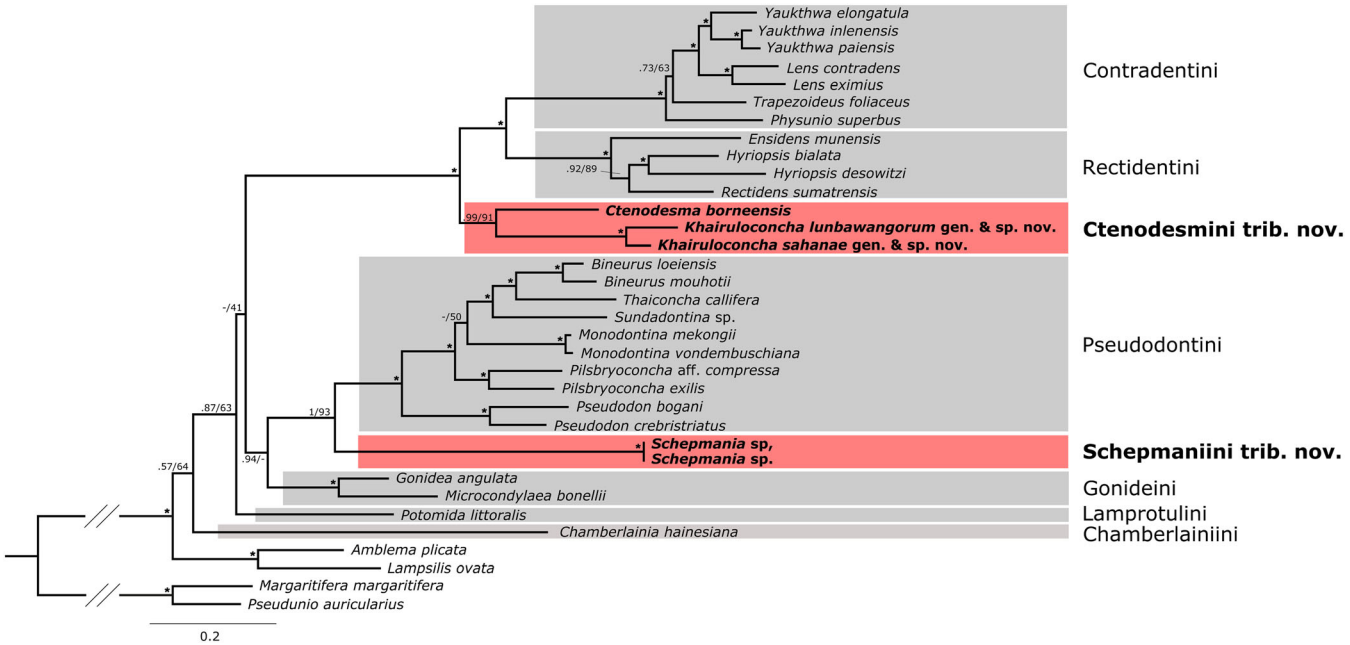

FIGURE 5 Maximum likelihood phylogenetic reconstruction (COI + ND1 + 16S + 18S + 28S) of the Gonideinae (shaded) with support values listed as posterior probabilities/ultrafast bootstraps (PP/UF). Values of PP and UF ≥ 95 are marked with "*". Newly sequenced, Bornean endemic specimens in bold and shaded in red

the tribe Lamprotulini (Unionidae, Gonideinae) (Pfeiffer, Breinholt & Page, 2019; Graf & Cummings, 2021b). Our phylogeny robustly recovers *Schepmania* as a member of a previously unrecognized lineage of the Gonideinae that we describe here as the Schepmaniini trib. nov.

This new tribe includes only the genus *Schepmania*, which consists of two species, *Schepmania niewenhuisi* (Schepman, 1898) and *Schepmania parcesculpta* (Martens, 1903) (Haas, 1969; Graf & Cummings, 2007; Zieritz et al., 2018b; Zieritz et al., 2020b; Graf & Cummings, 2021b). These two taxa are morphologically very similar but are thought to be distinguished based on the degree of sculpturing on the posterior ridge – with *S. niewenhuisi* being more heavily sculptured than *S. parcesculpta* (Figure 2) (Haas, 1969). However, the minor reported differences between these putative species are based on few specimens and there is doubt about whether the two nominal taxa represent distinct species (Haas, 1969). The sequenced specimens clearly belong to the genus *Schepmania* but because of uncertainties surrounding the validity and distributions of *S. niewenhuisi* and *S. parcesculpta*, we cannot confidently assign our specimens to either species. Further research focused on specimens from near the type localities of *S. niewenhuisi* (Bloe-oe, East Borneo (=Mahakam River, East Kalimantan, Borneo, Indonesia)) and *S. parcesculpta* (Guleh-Fluss, Ost Borneo (=river near Sangkulirang, East Kalimantan, Borneo, Indonesia)) will be necessary to resolve the systematics of *Schepmania*.

Tribe Ctenodesmini trib. nov. Pfeiffer, Zieritz, Rahim & Lopes-Lima.

Type Genus: *Ctenodesma* Simpson, 1900.

Diagnosis: The Ctenodesmini is morphologically very similar to its sister group, which consists of the tribes Contradentini and Rectidentini. The Ctenodesmini can be distinguished from the Contradentini by its tetragenous brooding condition (*vs*. ectobranchous brooding in Contradentini). The Ctenodesmini can be distinguished from the Rectidentini by its sculptured shells disc (*vs*. smooth in Rectidentini).

Distribution: Borneo.

Genera:

Ctenodesma Simpson, 1900

Khairuloconcha Zieritz, Lopes-Lima and Pfeiffer gen. nov.

Remarks: The higher-level classification of *Ctenodesma* has also varied substantially over the past 50 years, including placement in the Margaritiferidae (Starobogatov, 1970; Bogatov, Prozorova & Starobogatov, 2003), the subfamily Unioninae (Unionidae) (Haas, 1969), Unionidae *incertae sedis* (Graf & Cummings, 2007; Lopes-Lima et al., 2017; Zieritz et al., 2018b), a member of the Rectidentini (Unionidae, Gonideinae) (Pfeiffer, Breinholt & Page, 2019; Pfeiffer et al., 2021; Graf & Cummings, 2021b) or an unnamed sister group to the Rectidentini (Zieritz et al., 2020b). The topology recovered here suggests that *Ctenodesma* and its sister taxon *Khairuloconcha* represent a previously unrecognized tribe-level clade of the Gonideinae, described here as the Ctenodesmini trib. nov.

Khairuloconcha gen. nov. Zieritz, Lopes-Lima & Pfeiffer.

Type species: *Khairuloconcha lunbawangorum*

Diagnosis: Morphologically similar to its sister clade *Ctenodesma* but tends to have a sharper posterior ridge with nodulous sculpturing especially dorsally (*vs*. rounded and smooth posterior ridge in *Ctenodesma*), and has faint zigzag or irregular sculpture on the posterior slope (*vs*. uniform plications in *Ctenodesma*).

Description: Ovate shell outline, dorsal and ventral margins straight, largely parallel, dorsal margin angled slightly upwards, anterior end broadly rounded, posterior end narrowly rounded to broadly rounded. Posterior ridge somewhat distinct, often with small nodulous sculpture. Posterior slope gradual, bi- or triangulate with faint zigzag or irregular sculpturing. Yellowish-brown periostracum, occasionally with two or three green rays associated with ridges on posterior slope. Umbo slightly elevated above hinge line. Umbo sculpture zigzag with small nodules. Left valve with two straight, long, thin, slightly diverging lateral teeth. Left valve with one long, thick, crenulate or finely fractured pseudocardinal tooth. Right valve with one straight, long, thin lateral tooth. Right valve with two long pseudocardinal teeth, posterior pseudocardinal tooth much longer and thicker than the anterior pseudocardinal tooth. Nacre iridescent, faintly bluish or purplish, translucent.

Distribution: Northern Borneo.

Remarks: Morphologically very similar to *Ctenodesma* (Figure 2) but is molecularly very divergent (13.25–13.71% uncorrected p-distance; Figure 5).

Etymology: The species is named in honour of Dr Khairul Adha A. Rahim, one of Borneo's leading aquatic biologists and Senior Lecturer at the Universiti Malaysia Sarawak.

Khairuloconcha lunbawangorum sp. nov. Zieritz, Rahim, Taha & Pfeiffer.

Type locality: A small stream near Kuala Medalam (local name: Sungai Kemadi), Limbang drainage, Sarawak, Borneo, Malaysia (Figure 2c in Zieritz et al., 2020b).

Types: Holotype, FRST_MFw_X439 (transferred from UNIMAS X439 of Zieritz et al., 2020b (UNIMAS = Universiti Malaysia Sarawak)). Paratypes, FRST_MFw_X438 (n = 2, transferred from UNIMAS X438 and X440 of Zieritz et al., 2020b), same location as holotype.

Diagnosis: *Khairuloconcha lunbawangorum* is distinguished from its sister species *K. sahanae* by its more narrowly pointed posterior end (*vs*. broadly rounded in *K. sahanae*) and its less sharply defined and less nodulous posterior ridge (*vs*. sharper and more nodulous posterior ridge in *K. sahanae*) and less obvious sulcus.

Description: Ovate shell outline, dorsal and ventral margins straight, largely parallel, dorsal margin angled slightly upwards, anterior end broadly rounded, posterior end narrowly rounded. Posterior ridge somewhat distinct, often with small nodulous sculpture. Posterior slope gradual, bi- or triangulate with faint zigzag or irregular sculpturing, yellowish-brown periostracum, occasionally with two or three green rays associated with ridges on posterior slope, occasionally with faint green rays on shell disc. Umbo slightly elevated above hinge line. Umbo sculpture zigzag with nodules. Left valve with two straight, long, thin, slightly diverging lateral teeth. Left valve with one long, thick, crenulate or finely fractured

pseudocardinal tooth. Right valve with one straight, long, thin lateral tooth. Right valve with two long pseudocardinal teeth, posterior pseudocardinal tooth much longer and thicker than the anterior pseudocardinal tooth. Nacre iridescent, faintly bluish, translucent. Excurrent aperture longer than incurrent, multiple rows of small conical papillae. Incurrent aperture smooth, shorter than excurrent. Tetragenous brooding.

Distribution: Sungai Kemadi in Limbang River basin.

Etymology: The species is named in honour of the Lun Bawang people, an ethnic group indigenous to parts of the Bornean highlands, including the type locality.

Remarks: This species is known from only three specimens from one location. Sampling additional populations and individuals will be necessary to describe more completely the species' distribution and morphological variation.

Khairuloconcha sahanae sp. nov. Zieritz, Jainih & Lopes-Lima.

Type locality: A small stream (Sungai Dayang) within the Gomantong Forest Reserve, Kinabatangan drainage, Sabah, Borneo, Malaysia (Figure 3a).

Types: Holotype, BOR/MOL 14416. Paratype, FMNH 116932 (n = 1), Gomantong, Sandakan Residency, North Borneo.

Diagnosis: *Khairuloconcha sahanae* is distinguished from its sister species *K. lunbawangorum* by its more broadly rounded posterior end (*vs.* narrowly rounded in *K. lunbawangorum*) and its more sharply defined and more nodulous posterior ridge (*vs.* rounder and less nodulous posterior ridge in *K. lunbawangorum*) and a more obvious sulcus.

Description: Ovate shell outline, dorsal and ventral margins straight, largely parallel, dorsal margin angled slightly upwards, anterior end broadly rounded, posterior end broadly rounded. Slight sulcus in shell disc. Posterior ridge distinct, with small nodulous sculpture. Posterior slope gradual, triangulate with faint irregular sculpturing. Yellowish-brown periostracum. Umbo very slightly elevated above hinge line. Umbo sculpture zigzag with nodules. Left valve with two straight, long, thin, slightly diverging lateral teeth. Left valve with one long, thick, crenulate or finely fractured pseudocardinal tooth. Right valve with one straight, long, thin lateral tooth. Right valve with two long pseudocardinal teeth, posterior pseudocardinal tooth much longer and thicker than the anterior pseudocardinal tooth. Nacre iridescent, faintly purplish, translucent.

Distribution: Tributaries of lower Kinabatangan River basin but known only from one stream.

Etymology: The species is named in honour of the late Dr Sahana Harun, a dedicated lecturer and freshwater ecologist at the Institute of Tropical Biology and Conservation, Universiti Malaysia Sabah, Malaysia.

Remarks: This species is known from only two specimens (BOR/MOL 14416 and FMNH 116932). Both lots were collected from the Gomantong Hill area, which features only one stream (Sungai Dayang; personal communication R. Amandus, Gomantong Forest Reserve); however, the exact sampling location of FMNH 116932 is unknown. Sampling additional populations and individuals will be necessary to more completely describe the species' distribution and morphological variation.

4 | DISCUSSION

4.1 | A new genus and two new, rare freshwater mussel species endemic to Borneo

This study has revealed the presence of a new genus of freshwater mussel endemic to Borneo that comprises two rare species with highly restricted distributions: *Khairuloconcha lunbawangorum* within the Limbang River basin, Sarawak, and *K. sahanae* within the Kinabatangan River basin, Sabah. These species are very poorly understood and records of both have been previously identified as *Ctenodesma borneensis* (UNIMAS X438-X440 = *K. lunbawangorum*; FMNH 116932 = *K. sahanae*). Molecular phylogenetic analysis showed that *Khairuloconcha* is a divergent lineage sister to *C. borneensis*, and can morphologically be discriminated from *C. borneensis* by its sharper posterior ridge with nodulous sculpturing (especially dorsally) and a faint zigzag or irregular sculpture on the posterior slope rather than uniform plications. Based on the limited distribution data available to date, *Khairuloconcha* appears to be present in northern Borneo, whilst *Ctenodesma* may be restricted to western Borneo.

Both *Khairuloconcha* species as well as *Schepmania* sp. were each found only at a single site, with *K. lunbawangorum* and *K. sahanae* occurring in very low densities (i.e. three specimens per 4 person-hours and one specimen per 15 person-hours, respectively). Their habitats were similar, i.e. cool headwater streams situated in dense primary or secondary forest with natural bank vegetation, and characterized by near neutral pH. Nutrient concentrations were, however, elevated at both sites and especially at Gomantong (see Figure 4).

The Sungai Dayang, where *K. sahanae* was found, is located in the Class I – Protection Forest Reserve 'Gomantong' (Figure 6a) and as such, is protected by law from any form of land conversion or timber exploitation. As this stream exclusively receives water from the Gomantong Caves and surrounding hills within the Forest Reserve (personal communication R. Amandus, Gomantong Forest Reserve), the elevated nutrient concentrations in the water possibly stem from excrements of the dense avian and mammalian fauna of the forest (Lundberg & McFarlane, 2012; and references therein). However, the Gomantong Forest Reserve is small (approx. 3,297 ha Class I + 1,816 ha Class VI in the centre, including the Gomantong Caves) and is surrounded by large areas of oil palm plantations with very high rates of historical, recent and continuing deforestation (Figure 6a). The nearest oil palm plantation and mill are located less than 3 and 15 km from the sites where *K. sahanae* was found, respectively (Figure 6a). Considering the very low population density observed, it is therefore possible that this species is already threatened by continuing habitat deterioration, potentially associated with logging and land-use change in the surrounding catchment.

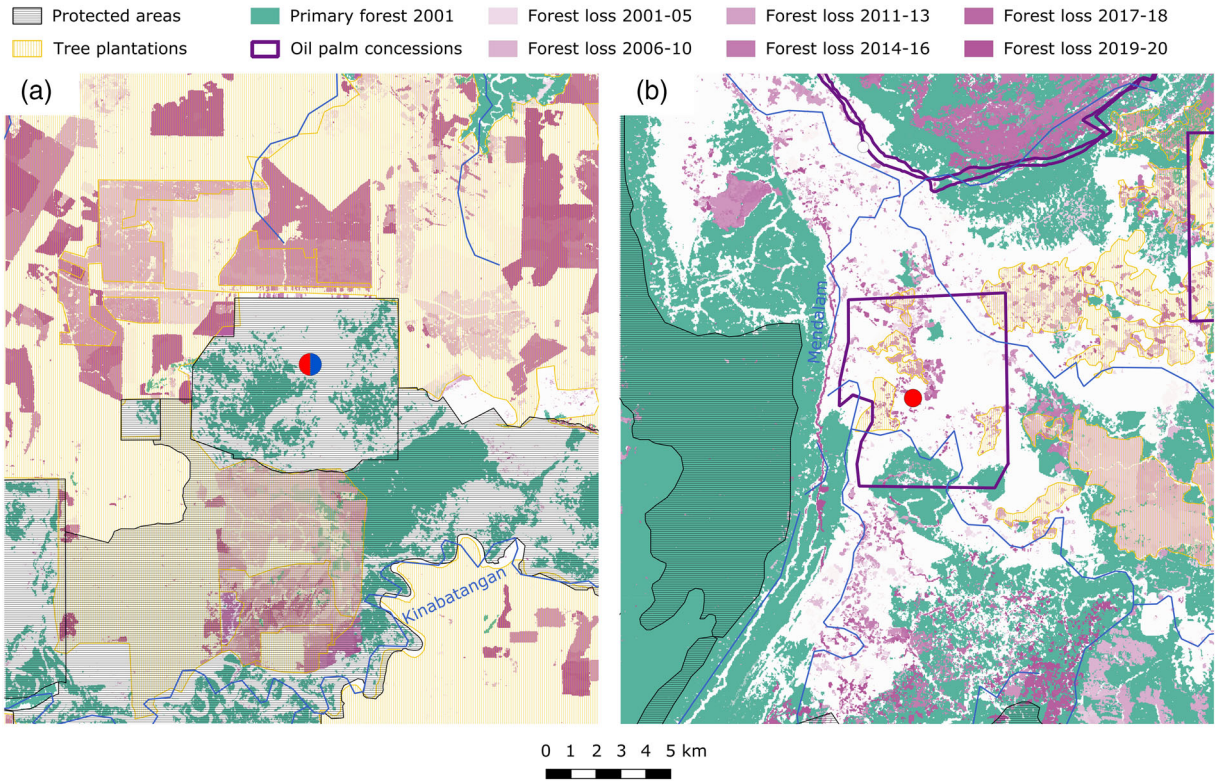

FIGURE 6 Land cover and land use of areas surrounding the two recently confirmed locations (in 2018 and 2019) of endemic freshwater mussel species populations, i.e. (a) *Khairuloconcha sahanae* sp. nov. (red) and *Schepmania* sp. (blue) at the Gomantong Protection Forest Reserve, and (b) *Khairuloconcha lunbawangorum* sp. nov. (red) in the upper Limbang River catchment. Data sources: Forest loss, Hansen/UMD/Google/USGS/NASA (Hansen et al., 2013); Oil palm concessions, World Resources Institute (2014); Primary forest 2011, Turubanova et al. (2018); Protected areas, UNEP-WCMC & IUCN (2014–2020); Tree plantations, Harris, Goldman & Gibbes (2019)

The situation is particularly alarming for *K. lunbawangorum*, as its single known population is situated in an unprotected area that has been allocated for an industrial-scale oil palm plantation (Figure 6b). Although the population was found in a stream within a secondary forest, deforestation is continuing and land-use conversion to oil palm plantation has already commenced in the immediate vicinity of the site (Figure 6b), presenting an immediate threat of extinction to *K. lunbawangorum*.

4.2 | Evolutionary biogeography

Khairuloconcha appears to have undergone a recent divergence (speciation), a diversification pattern that is not common in the freshwater mussel genera native to Borneo which, based on currently available data, are frequently represented by a single species on the island (e.g. *Caudiculatus caudiculatus* (Martens, 1867), *Discomya radulosa* (Drouët & Chaper, 1892), *Elongaria trompi* (Drouët & Chaper, 1892), *Hyriopsis velthuizeni* (Schepman, 1896), *Pressidens exanthematicus* (Küster, 1861)). We suspect that this may be related to the habitat and host fish requirements of species within *Khairuloconcha*, which, in contrast to most other known freshwater mussels in Borneo, appear to be restricted to headwater streams (Zieritz & Lopes-Lima, 2018; Zieritz et al., 2018c). Using headwater fish species as hosts for their parasitic larvae (glochidia) would be expected to strongly restrict dispersal between river (sub)basins, thus potentially leading to reproductive isolation of populations and ultimately, divergence of species. Potential *Khairuloconcha* spp. host fish species include the cyprinids *Nematabramis borneensis*, *Nematabramis everetti* and *Rasbora* spp., all of which are commonly found in headwater streams of Sarawak and Sabah (Sulaiman & Mayden, 2012; Ng et al., 2017). The fact that the only two *Khairuloconcha* populations known to date represent separate species suggests that more, yet undescribed species of this genus and potentially other endemic mussel taxa may exist in other headwater streams across Borneo, particularly those situated within functioning rainforest habitat. It should be a priority to locate such populations and facilitate the protection of their habitats.

The Bornean endemic freshwater mussel taxa sequenced to date fall into two newly described clades that are endemic to Borneo, i.e. Schepmaniini and Ctenodesmini. Our dataset thus increases the number of Gonideinae tribes from six (Pfeiffer, Breinholt & Page, 2019) to eight and provides further evidence for the importance of Borneo as an evolutionary hotspot for freshwater biodiversity (de Bruyn et al., 2014). A recent fossil-calibrated mitogenome phylogeny (Zieritz et al., 2020a) placed the split of the Contradentini

and Rectidentini, and the Gonideini and Pseudodontini, at 79 and 95 mya, respectively. Assuming these node ages, the two Bornean endemic tribes split from their respective sister tribes with a predominantly mainland–Southeast Asian distribution some time in the late Cretaceous, i.e. the Ctenodesmini from Contradentini + Rectidentini, and the Schepmaniini from Pseudodontini (Figure 5). According to palaeogeographical reconstructions (Figure 3.4 in Hall, 2012), at that time western Borneo was connected by land (i.e. the Sunda Shelf) with today's mainland Southeast Asia as well as eastern Sumatra and Java, with significant elevations (highlands) from the Belitung Islands in the west to what is now the lower Kapuas River in the east. These highlands may have created an effective dispersal barrier for freshwater mussel populations, which could have led to a divergence of the Ctenodesmini and Schepmaniini in the river basin(s) east of these highlands from their respective sister clades.

4.3 | Recommendations for conservation

The anecdotal evidence collected indicates that historically, at least *Schepmania* sp. probably used to be widely distributed across the lower Kinabatangan basin and adjacent coastal basins, but that most of these populations have been lost within the last 50 years or so. These populations may have been extirpated in the course of deforestation campaigns in Sabah, which reached industrial scale and devastation in the 1980s and 1990s, and are particularly intense in the Kinabatangan basin (Seda, 1993; Bryan et al., 2013). A similar situation is likely to be true for *K. sahanae*, but this species is small and difficult to discriminate from young *Schepmania* sp. for laymen, preventing us from gathering reliable information on its historical distribution.

In light of the rapid pace of destruction of forest stream habitat in Borneo, it is of utmost urgency that forest stream and other freshwater habitats across the island are surveyed to identify yet unknown populations and potentially, even species, of endemic Unionidae, and characterize and monitor their distribution and population characteristics. Particular attention should be paid to surveying rivers in protected areas or other areas of largely undisturbed habitat, including the National Parks of Gunung Buda and Gunung Mulu in Sarawak, and Danau Sentarum and Sebangau National Parks in Kalimantan. The speed of data collection could be increased significantly by complementing traditional physical surveys with environmental DNA (metabarcoding) surveys, which could also be used at otherwise inaccessible sites (e.g. owing to the presence of crocodiles) but has rarely been used in the tropics (Ruppert, Kline & Rahman, 2019; Prié et al., 2020). Wherever possible, these surveys should also include collection of data on mussel ecology and biology, including those on habitat requirements, potential threats and population structure, which will provide a critical basis on which targeted conservation measures can be developed.

Considering the limited resources available for this herculean task, it is likely that a large number of populations and species will have already disappeared before they will have been located and subsequently protected. Parallel to continuing survey efforts, we therefore recommend that an action plan to save the Bornean endemic freshwater mussel species should be urgently developed and implemented. First and foremost, to maximize the chances of survival of *K. lunbawangorum*, the Sungai Kemadi, including its surrounding remaining forest habitats (Figure 6b), should immediately be placed under legal protection (e.g. declaration as a 'High Conservation Value Area') that prohibits deforestation and land use conversion to agricultural land. Considering the very small sizes of both *Khairuloconcha* populations, environmental conditions and population characteristics (including levels of recruitment) should be monitored regularly at both Sungai Kemadi and Sungai Dayang. Ideally, these measures of habitat protection and further survey efforts should be accompanied by captive breeding programmes for reintroduction and augmentation. This will require identification of host fish species and data gathering on reproductive cycles and specific habitat requirements.

Wider conservation actions across all Bornean states should focus on mitigating the impacts of deforestation and palm plantations by establishing riparian buffer zones, which are required by law (i.e. Sabah 5–20 m, Sarawak 5–50 m, Indonesia 50–200 m, depending on river width) but are often not implemented (Figures 3b and d) (Luke et al., 2019). Outreach programmes, including citizen science projects, will be needed to improve awareness of stakeholders, decision makers and the general public about Borneo's unique freshwater mussel diversity and the important ecosystem services they provide (Irvine et al., 2016; Zieritz et al., 2018a).

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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