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A glimpse in the dark? A first phylogenetic approach in a widespread freshwater snail from tropical Asia and northern Australia (Cerithioidea, Thiaridae)

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Abstract

Thiaridae are a speciose group of freshwater snails in tropical areas including a high number of described nominal taxa for which modern revisions are mostly lacking. Using an integrative approach, the systematic status of a group of thiarids from the Oriental region, including the nominal species *Melania aspera* and *M. rudis*, is reassessed on the basis of shell morphology and biometry, radula dentition patterns, and reproductive biology along with molecular genetic methods. Our results suggest that populations from the Oriental region cannot be distinguished on the basis of shell morphology, radula characters and their reproductive mode and are monophyletic based on mitochondrial sequences. Hence, *M. rudis* with *M. aspera* are regarded as belonging to the same species along with several other nominal taxa that were previously included in *M. rudis*. Moreover, populations from Thailand and Australia, from where the species was not previously recorded, could be shown to form a monophyletic group together with samples from Indonesia. However, a generic affiliation with *Thiara*, in which the investigated taxa were often included in the past, was not supported in our phylogenetic analyses, highlighting the need for a comprehensive revision of the genus-group systematics of Thiaridae as a whole.

Key Words

Cerithioidea, evolutionary systematics, Oriental region, Thailand

Introduction

Despite advances in the understanding of the family-level phylogeny of Cerithioidea Fleming, 1822, the taxonomical diversity in Thiaridae Gill, 1871 (1823) is still not well understood, and evolutionary systematic research in the sense of Glaubrecht (2010) in this particular family is still in its infancy. The Thiaridae, in earlier treatments subsumed under the name Melaniidae Children, 1823, have been used as a "rubbish bin" to accommodate all freshwater lineages belonging to the Cerithioidea. Only after the removal of the families Pachychilidae Fischer & Crosse, 1892, Melanopsidae Adams & Adams, 1854, Paludomidae Stoliczka, 1868, Pleuroceridae Fischer, 1885 (1863), and Semisulcospiridae Morrison, 1952) (Campbell 2019; Neiber and Glaubrecht 2019b, 2019c, 2019d; Strong and Lydeard 2019 and references therein) and recently the Neotropical Hemisinidae Fischer & Crosse, 1891 (Glaubrecht and Neiber 2019a), a more accurate circumscription of "core" Thiaridae began to emerge on the basis of molecular and/or morphological evidence (e.g., Glaubrecht 1993, 1996, 2011; Holznagel and Lydeard 2000; Lydeard et al. 2002; Glaubrecht et al. 2009; Strong 2011; Strong et al. 2011).

In addition to uncertainties in the delimitation of genera, research on thiarids is further complicated by the large disparity of shell characters among species, a large phenotypic plasticity within species and a high ecological adaptability that is, however, also known from other limnic Cerithioidea. This conchological variability has certainly led to an overestimation of the number of species in the past, as specifically shown for limnic lineages in the superfamily (Glaubrecht 1993, 1996; Köhler and Glaubrecht 2001, 2003, 2006; Glaubrecht and Köhler 2004; Glaubrecht et al. 2009), but may also cause problems in delimiting species resulting in an underestimation of the actual morphological disparity versus the taxonomical diversity, at least in some cases. These problems are exacerbated by the putatively widespread occurrence of parthenogenesis in different lineages of Thiaridae (Glaubrecht 1996) and the associated problems of what is actually meant by "species" in this case (e.g. Hausdorf 2011). Additionally, Thiaridae have also realised different life history strategies that were characterised by Glaubrecht (1996, 1999, 2006, 2011) by the duration of ontogenetic stages to remain within a specialised structure of the female, viz. the subhaemocoelic brood pouch. While in some thiarids only very early ontogenetic stages, i.e. embryos without shell, develop and are released as veligers (ovoviviparity), other thiarid species brood and even transform their subhaemocoelic brood pouch into a matrotrophic organ or "pseudoplacenta" that apparently nourishes the developing juveniles, as e.g. in the Southeast Asian thiarid *Tarebia granifera* (Lamarck, 1816) (euviviparity, see Glaubrecht 1996; Glaubrecht et al. 2009; Maaß and Glaubrecht 2012; Veeravechsukij et al. 2018b). Finally, some thiarids also have an extraordinarily high invasive potential, such as *Melanoides tuberculata* (Müller, 1774) and *Tarebia granifera* and today have an almost pantropical distribution (e.g., Brown 1994; Glaubrecht 1996).

To date, only few of the several dozen thiarid taxa have seen closer investigation. Glaubrecht et al. (2009) and Maaß and Glaubrecht (2012) surveyed the thiarid fauna of Australia. Dechruska et al. (2013) evaluated the status and identity of the nominal taxon *Melania jugicostis* Hanley & Theobald, 1876 from the Southeast Asian mainland, and Veeravechsukij et al. (2018a, 2018b) investigated the phylogeography and reproductive biology of *T. granifera* and its trematode parasites. However, many other named taxa have been rarely studied and, thus, remain enigmatic and even pure nomenclatorial "ghosts" with highly questionable status as evolutionary relevant entities, which hampers further insights into the systematics, biogeography, and evolution of these freshwater gastropods otherwise under scrutiny, e.g., in speciation and/or radiation studies.

Melania aspera Lesson, 1831, which was originally described from New Guinea (Lesson 1830–1831), is such an "enigmatic" taxon (Fig. 1), which Glaubrecht and Podlacha (2010) regarded as a possible senior synonym of the nominal species *Melania rudis* Lea & Lea, 1851. The latter taxon is usually regarded as belonging to *Thiara* Röding, 1798 and thought to be relatively widespread, being reported from several countries, occurring from India and Sri Lanka to Southeast Asia and the Indo-Australian archipelago (Schepman 1892, 1915; Rensch 1934; van Benthem Jutting 1937; Subba Rao 1989; Ramakrishna and Dey 2007; Budha 2010; Patil and Talmale 2011, see also Fig. 2). However, actual distribution records are relatively scarce in the literature and the distinction from other nominal thiarid taxa remains uncertain so far.

As a further contribution towards a better understanding of thiarid diversity, we here re-evaluate the identity of *M. aspera* and *M. rudis* on the basis of museum samples including available type material as well as material collected during ongoing surveys in Southeast Asia using shell morphology and biometry, radula dentition patterns, and reproductive biology along with molecular genetic methods. Nomenclatural issues and the synonymy of the genus *Thiara* are also discussed.

Material and methods

This study is mainly based on the examination of specimens in the collections of the Parasitology and Medical Malacology Research Unit, Department of Biology, Faculty of Science, Silpakorn University, Thailand and the Museum für Naturkunde, Berlin, Germany, and supplemented by material from other museums (see below). Additionally, new samples were collected using hand picking and scooping methods in Thailand and Australia. Specimens were fixed in 75–96% ethanol.

Collection acronyms

MNHN Muséum National d'Histoire Naturelle de Paris, France
SUT Silpakorn University, Nakhon Pathom, Thailand
USNM National Museum of Natural History, Washington, USA
ZMB Museum für Naturkunde, Berlin, Germany (formerly Zoologisches Museum Berlin)

Coordinates (WGS84) of localities were taken with a GPS device or determined as accurately as possible from a map. Sampling sites were then mapped on a dot-by-dot basis to a digitally reduced version of the drainage pattern map of the Indo-Australian region. This map was prepared using a relief map on the basis of the Global30-Arc-Second Elevation Data (GTOPO30) from the U.S. Geological Survey and a river map from the map server Aquarius Geomar; and then compiled using Adobe Photoshop CS3 and Adobe Illustrator. For the exact locality data, see the material examined section.

Shell characters

Specimens were photographed using a digital EOS 350D camera (Canon, Tokyo, Japan). Standard biometric parameters were taken from each shell using electronic cal-

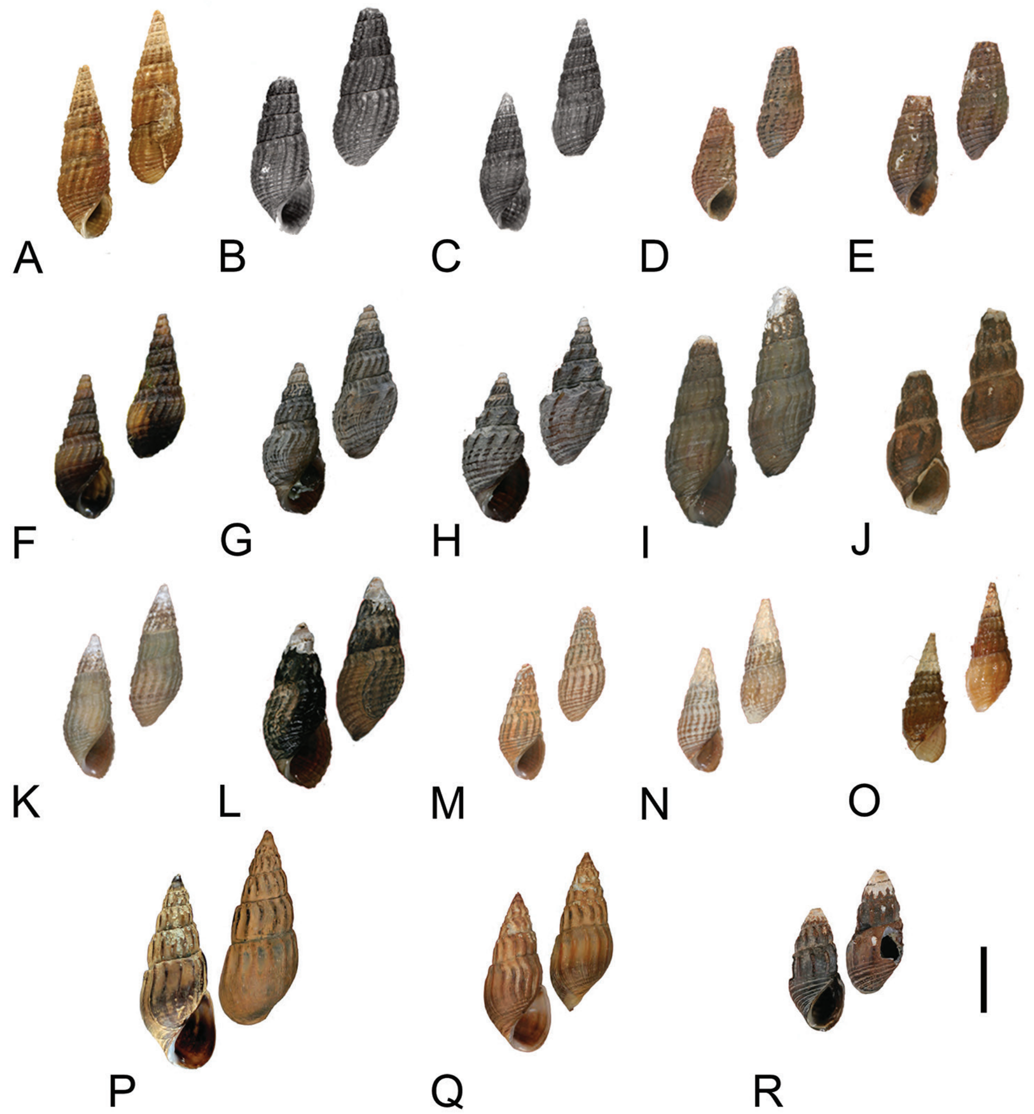

Figure 1. Shells of "*Thiara*" *aspera* (Lesson, 1831). **A**. Holotype of *Melania aspera* Lesson, 1831, MNHN 21098, 'La Nouvelle-Guinée' [more specifically Manokwari on New Guinea Island, West Papua, Indonesia, see Glaubrecht and Podlacha 2010]; **B.** Syntype of *Melania rudis* Lea & Lea, 1851, USNM 119778, Amboyna; **C.** Syntype of *Melania microstoma* Lea & Lea, 1851, USNM 119722, mountain streams, isle of Negros, Philippines; **D.** ZMB 107002, Calcutta, India; **E.** ZMB 107003, Ceylon, Sri Lanka; **F.** ZMB 127534, Don Ko Canal, Nakhon Pathom, Thailand; **G.** ZMB 127535, Don Ko Canal, Nakhon Pathom, Thailand; **H.** ZMB 127535, Don Ko Canal, Nakhon Pathom, Thailand; **I.** ZMB 191279, Yehembang River, Bali, Indonesia; **J.** ZMB 191279, Yehembang River, Bali, Indonesia; **K.** ZMB 106472, Yehembang, Bali, Indonesia; **L.** East of Mendaya, stream southwest of Gumicik, Bali, Indonesia; **M.** ZMB 191278, stream at Tembeeha, road Tirobus-Kendari, Southwest Sulawesi, Indonesia; **N.** ZMB 107378, Banggai Islands, Peleng Island, West of Peninsula, Tataban river, Central Sulawesi, Indonesia; **O.** ZMB 107377, Banggai Islands, Peleng Island, West of Peninsula, Tataban river, Central Sulawesi, Indonesia.river; **P, Q.** ZMB 107617, Wabalarr, Roper River, Northern Territory, Australia; **R.** ZMB 106599, Berry Springs, Northern Territory, Australia. Scale bar: 1 cm.

lipers (accuracy 0.1 mm): shell height (H), shell width (W), aperture length (AL; measured from the upper apertural angle to the farthest point on the basal margin of the aperture), aperture width (AW; measured perpendicular to AL as the widest distance between outer apertural margin and outer margin of parietal callous), height of the body whorl (BW), and number of whorls (NW) as shown in Figure 3A. To reduce dimensionality a principal component analysis was conducted on log-transformed shell measurements using R 3.3.2 (R Core Team 2016). Only the minimal number of PCA axes that accounted for more than 95% of the cumulative variation were used for further testing.

The Shapiro-Wilk test was conducted in R to test for normal distributions of PCA 1 and PCA 2 values, respectively, for the here proposed geographic subgroups, i.e., samples from 1) Thailand, 2) Indonesia, 3) India, and Sri Lanka, and 4) Australia. Since some of the Shapiro-Wilk tests were significant ($p \leq 0.05$), the non-parametric Kruskal-Wallis rank sum test was conducted for PCA 1 and

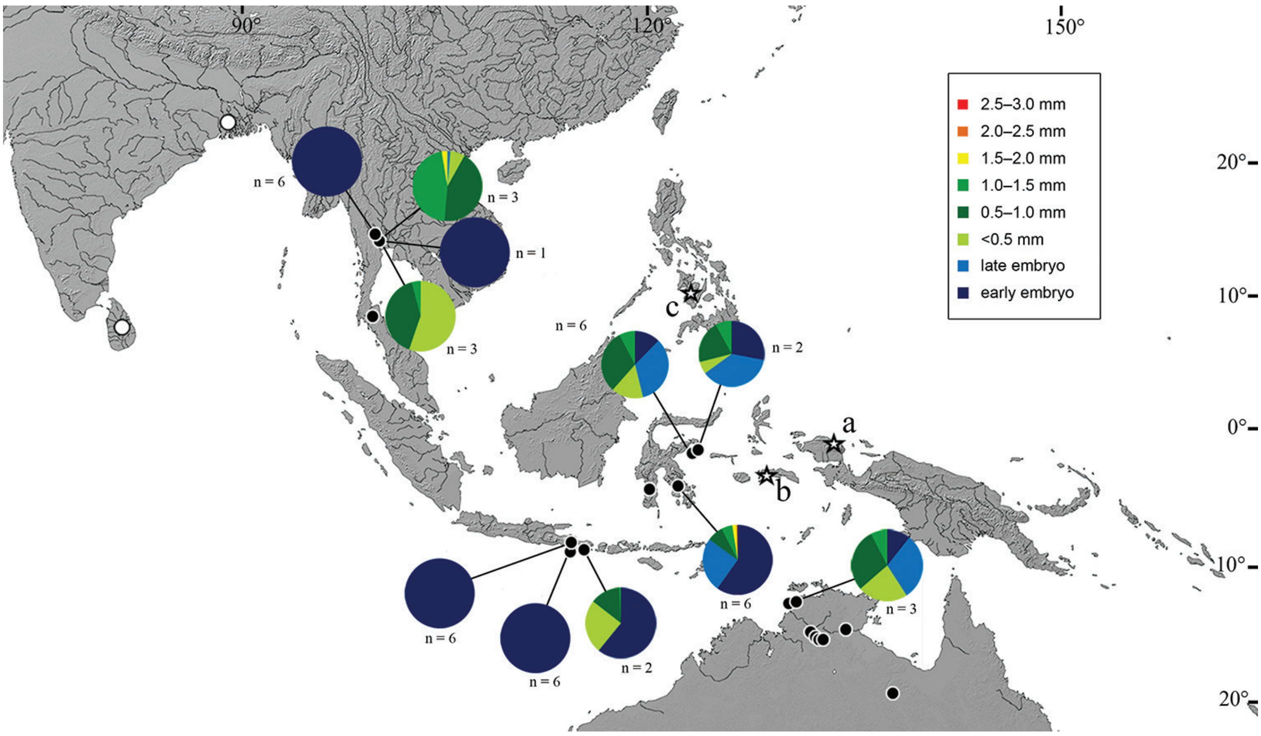

Figure 2. Distribution and reproductive strategy of "*Thiara*" *aspera* (Lesson, 1831). Stars: type localities of a) *Melania aspera* Lesson, 1831, Monokwari, New Guinea, b) *Melania rudis* Lea & Lea, 1851, Amboyna and c) *Melania microstoma* Lea & Lea, 1851, mountain streams, isle of Negros, Philippines. Pie charts show the percentages of offspring in the brood pouch of female *T. aspera* in different size classes as defined in Glaubrecht et al. (2009), see inset. The numbers near the pie charts refer to the number of individuals examined per population. Filled circles: material preserved in ethanol; open circles: dry shells.

PCA 2 assuming the grouping of specimens according to geography followed by Dunn's test (Bonferroni-corrected) as post-hoc test as implemented in the R package "dunn.test 1.3.5" (Dinno 2017) in case that the Kruskal-Wallis-rank-sum tests were significant.

Radula preparation

Shells of representative specimens were cracked with a small vice and removed from the soft body parts, which were afterwards examined and dissected with the aid of a Leica Wild MZ 9.5 stereo microscope (Leica Microsystems, Wetzlar, Germany). Radulae were extracted following the protocol of Holznagel (1998), fixed on aluminium stubs, and coated with platinum using a Polaron SC 7640 Sputter Coater (Quorum Technologies, East Grinstead, UK). Radulae were then viewed and photographed (oriented so that denticles on the teeth were well visible) with a scanning electron microscope (SEM) EVO LS10 (Zeiss, Oberkochen, Germany).

Content of brood pouch

The brood pouch was opened after removing the mantle and its content was counted under a Leica Wild MZ 9.5 stereo microscope. Both, shelled juveniles and embryos, were grouped into standard size classes as described in Glaubrecht et al. (2009). Embryos and juveniles from representative specimens were fixed on aluminium stubs, air-dried, coated with platinum using a Polaron SC 7640 Sputter Coater, and then viewed, photographed, and measured (Fig. 3B) with a EVO LS10 SEM. Parameters of the embryonic shell were measured from SEM images as shown in Figure 3B: diameter of first half whorl (de; measured as the maximal witdth of the shell after 0.75 turns of the suture line), width of first quarter whorl (he; measured parallel to de as the distance from the starting point of the suture to the point after 0.25 turns of the suture line), width of first half whorl (we; measured perpendicular to de as the distance from the starting point of the suture to the point after 0.5 turns of the suture line).

Molecular methods and phylogenetic analyses

Total genomic DNA was extracted from ethanol-preserved foot muscle tissue using a CTAB protocol as described by Winnepenninckx et al. (1993) from 31 thiarid specimens and *Paludomus siamensis* Blanford, 1903 as outgroup representing one of the cerithioidean families, which have been shown to be closely related to the Thiaridae (Wilson et al. 2004; Strong et al. 2011).

For phylogenetic analyses, fragments of the mitochondrial cytochrome c oxidase subunit 1 (*cox1*) gene and the

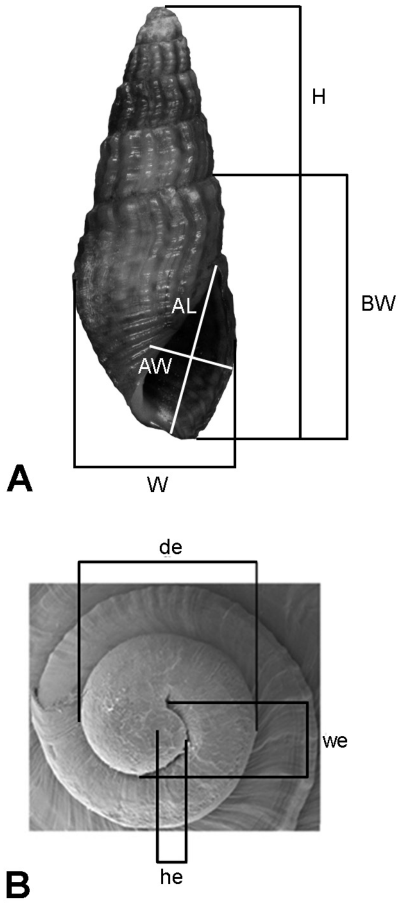

Figure 3. Measured shell parameters. **A:** H – shell height; W – shell width; BW – body whorl height; AL – aperture length; AW – aperture width. **B:** he – height of embryonic shell; we – width of embryonic shell; de – maximum diameter at one whorl.

16 S rRNA (16S) gene were amplified by polymerase chain reaction (PCR) using the primer pairs LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3'; Folmer et al. 1994) plus HCO2198var (5'-TAW ACT TCT GGG TGK CCA AAR AAT-3'; Rintelen et al. 2004) and 16S_F_Thia2 (5'-CTT YCG CAC TGA TGA TAG CTA G-3'; Neiber and Glaubrecht 2019a, see also Gimnich 2015) plus H3059var (5'-CCG GTY TGA ACT CAG ATC ATG T-3'; Wilson et al. 2004), respectively. Amplifications were conducted in 25 µl volumes containing 50–100 ng DNA, 1× PCR buffer, 200 mM of each dNTP, 0.5 mM of each primer and 1 U of *Taq* polymerase. After an initial denaturation step of 3 min at 94 °C, 35 cycles of 30 s at 94 °C, 60 s at 45–62°C and 60–120 s at 72°C were performed, followed by a final extension step of 5 min at 72°C. PCR products were purified using a NucleoSpin Extract II Kit (Macherey–Nagel, Bethlehem, PA, USA). Both strands of the amplified gene fragments were cycle-sequenced using the primers employed in PCR with the Big Dye Terminator chemistry version 1.1 (Applied Biosystems, Inc., Waltham, MA, USA). Sequences were visualised on an ABI 3130xl or ABI 3730xl Genetic Analyzer (Applied Biosystems, Inc.).

Forward and reverse sequence reads were assembled with CODONCODE ALIGNER v. 3.7.1 (CodonCode Corporation, Dedham, MA, USA) and corrected by eye. For information on vouchers, see Table 1. The protein coding *cox1* sequences were aligned with MUSCLE (Edgar 2004) as implemented in MEGA 6 (Tamura et al. 2013) under default settings. The 16S sequences of were aligned with MAFFT (Katoh and Standley 2013) using the Q-INS-i iterative refinement algorithm and otherwise default settings, because this algorithm has been described to perform better for the alignment of sequence data sets that may contain deletions and insertions than alternative multiple sequence alignment methods (Golubchik et al. 2007).

Maximum likelihood (ML), Bayesian Inference (BI), and maximum parsimony (MP) approaches were used to reconstruct the phylogenetic relationships. The sequence data set was initially divided into four partitions for the nucleotide model-based ML and BI approaches: 1) 1st codon positions of *cox1*, 2) 2nd codon positions of *cox1*, 3) 3rd codon positions of the *cox1*, and 4) the 16S. To select an appropriate partitioning scheme and evolutionary models the sequence data set was analysed with PARTITIONFINDER v. 1.1.1 (Lanfear et al. 2012) conducting an exhaustive search and allowing for separate estimation of branch lengths for each partition using the Bayesian information criterion as recommended by Luo et al. (2010). Models to choose from were restricted to those available in MRBAYES v. 3.2.6 (Ronquist et al. 2012) as well as in GARLI v. 2.1 (Zwickl 2006). As best-fit partitioning scheme, the PARTITIONFINDER analysis suggested to combine the 1st and 2nd codon positions of *cox1* and the 16S sequences together in one partition (GTR + G model) and the 3rd codon positions of *cox1* in a second partition (HKY + G model).

The BI analysis was performed using MRBAYES v. 3.2.6. Metropolis-coupled Monte Carlo Markov chain (MC^3) searches in MRBAYES were run with four chains in two separate runs for 50,000,000 generations with default priors, trees and parameters sampled every 1000 generations under default heating using the best-fit model as suggested by PARTITIONFINDER. Diagnostic tools in MRBAYES, including Estimated Sample Size (ESS) values > 200, were used to ensure that the MC^3 searches had reached stationarity and convergence. The first 5,000,000 generations of each run were discarded as burn-in.

Heuristic ML analysis was performed with GARLI using the best-fit models as suggested by PARTITIONFINDER. Support values were computed by bootstrapping (BS) with 1,000 replicates.

Heuristic MP searches were carried out with PAUP v. 4.0b10 (Swofford 2002) using 100 random-addition-sequence replicates and TBR branch swapping. Support values were computed by bootstrapping with 1,000 replications.

Alternative phylogenetic hypotheses were tested using the approximately unbiased (AU) test (Shimodeira 2002) as implemented in the program CONSEL (Shimodeira and Hasegawa 2001). Information on vouchers and GENBANK accession numbers are listed in Table 1.

Table 1. Museum registration numbers, GenBank accession numbers and locality data for the specimens used in the molecular phylogenetic analyses. Abbreviations for countries: AUS – Australia, IDN – Indonesia, IND – India, THA – Thailand.

Taxon	Museum number	Extraction number	Country	Latitude	Longitude	GenBank accession number	
						cox1	16 S rRNA gene
"Thiara" aspera	SUT 0311020	11449	THA	13°38'08"N	100°05'03"E	MK879291	MK879427
	SUT 0312070	11446	THA	13°48'08"N	100°02'06"E	MK879292	MK879428
	SUT 0311044	9603	THA	13°38'08"N	100°05'03"E	MK879290	–
	ZMB 191268	2200	IDN	03°39'28"S	122°13'52"E	MK879296	MK879434
	ZMB 191488	4558	IDN	08°38'39"S	115°16'38"E	MK879297	MK879435
	ZMB 107377	6494	IDN	01°32'18"S	122°51'28"E	MK879293	MK879429
	ZMB 107378	6495	IDN	01°32'18"S	122°51'28"E	MK879294	MK879430
	ZMB 107617	7586	AUS	14°56'02"S	133°10'26"E	MK879295	MK879433
	ZMB 107617	8743	AUS	14°56'02"S	133°10'26"E	–	MK879431
	ZMB 107617	8744	AUS	14°56'02"S	133°10'26"E	–	MK879432
"Stenomelania" denisoniensis	ZMB 106682	7599	AUS	14°55'47"S	133°08'44"E	MK879288	MK879425
	ZMB 106632	7602	AUS	15°00'42"S	133°14'25"E	MK879287	MK879424
Thiara amarula	ZMB 191489	2886	IDN	01°26'43"S	127°29'01"E	MK879289[a]	MK879426[a]
	ZMB 107472	6496	IDN	03°35'28"S	128°08'42"E	MK094074	MK098355
Thiara winteri	ZMB 106554	1043	IDN	08°23'38"S	114°45'04"E	MK879301	MK879439
	ZMB 190261	1055	IDN	02°35'34"S	120°54'10"E	MK879302	MK879440
Thiara cf. *winteri*	ZMB 106472	1001	IDN	08°23'38"S	114°45'04"E	MK879298	MK879436
	ZMB 191279	2232	IDN	08°23'36"S	114°45'04"E	MK879299	MK879437
	ZMB 191279	4559	IDN	08°23'36"S	114°45'04"E	MK879300	MK879438
Mieniplotia scabra	ZMB 107382	6514	IDN	00°48'33"N	127°17'40"E	MK879279	MK879416
	ZMB 107564	7340	AUS	14°55'38"S	133°07'06"E	MK879280	MK879417
	ZMB 127495	9574	THA	07°55'15"N	099°15'47"E	MK879285	MK879422
	SUT 0312060	9578	THA	12°51'15"N	099°59'49"E	MK879278	MK879415
	SUT 0311024	9580	THA	14°54'04"N	100°03'48"E	MK879276	MK879413
	SUT 0311040	9582	THA	13°25'07"N	099°57'18"E	MK879277	MK879414
	ZMB 127470	9589	THA	08°27'09"N	098°28'01"E	MK879284	MK879421
	ZMB 127468	9599	THA	12°56'54"N	099°28'52"E	MK879283	MK879420
	ZMB 107962	9779	THA	16°37'38"N	100°56'43"E	MK879282	MK879419
	ZMB 107869	9781	THA	08°38'18"N	099°44'59"E	MK879281	MK879418
	SUT 0311009	9787	THA	16°11'33"N	099°15'51"E	MK879275	MK879412
Melanoides tuberculata	ZMB 200313	7530	IND	11°34'45"N	076°34'55"E	MK879274	MK879411
Paludomus siamensis	ZMB 107721	7334	THA	14°26'15"N	098°51'11"E	MK879286	MK879423

[a] From Neiber and Glaubrecht (2019a).

Results

Biometric analyses

The first two principal components (PCA 1 and PCA 2) account for > 95% of the cumulative variation in shell parameters. The plot of PCA 1 vs PCA 2 (Fig. 4A) shows that the clusters of specimens that were grouped according to geographic origin widely overlap. Especially the clusters of specimens from Thailand and Indonesia (corresponding to mitochondrial Clades A and B, Fig. 4) and the clusters of specimens from Australia (corresponding to mitochondrial Clade C, Fig. 4) also widely overlap. The Kruskal–Wallis rank sum tests were significant for PCA 1 ($p < 5.0 \times 10^{-6}$) and PCA 2 ($p < 2.0 \times 10^{-16}$), i.e., at least one group stochastically dominates one other group in each of the tests. Dunn's test for PCA 1 found significant differences between the groups including samples from Indonesia and Australia ($p < 0.0001$) as well as between the groups including samples from Australia and Thailand ($p < 0.0075$), respectively, but not for pairwise comparisons of the other groups (Fig. 4B). Dunn's test for PCA 2 found significant differences between the following groups: Indonesia vs Australia ($p < 0.0031$), Indonesia vs Thailand ($p < 0.0001$), Australia vs Thailand ($p < 0.0007$), Australia vs India/Sri Lanka ($p < 0.0004$), and Thailand vs India/Sri Lanka ($p < 0.0001$), but not for Indonesia vs India/Sri Lanka (Fig. 4C). However, both for PCA 1 and PCA 2 the comparison of ranges shows that the ranges of all pairs of geographic groups overlap and therefore do not allow a diagnostic separation of these groups on the basis of the biometric data. The included type specimens of the nominal taxa *M. rudis* and *M. microstoma* fall within the convex hull spanned by specimens sampled from Thailand, Indonesia, Australia, India, and Sri Lanka in the PCA 1 vs PCA 2 plot; only the holotype of the nominal taxon *M. aspera* lies outside this area (Fig. 4A), although closely resembling the examined syntypes of *M. rudis* and *M. microstoma* with respect to shell sculpture and overall shape.

Phylogenetic analyses

A clade including *Thiara amarula* (Linnaeus, 1758) (the type species of *Thiara* Röding, 1798), *T. winteri* (Busch, 1842) in Philippi (1842–1844), *T.* cf. *winteri* from Bali, and the specimens identified as *Thiara aspera* from Thailand, Indonesia, and Australia as well as "*Stenomelania*" *denisoniensis* (Brot, 1877) in Brot (1874–1879) was recovered in all three analyses (BI: 1.00, BS (ML): 92, BS (MP): 96). However, *Thiara* is paraphyletic with respect to "*S*." *denisoniensis*. *Thiara amarula* grouped together with *T. winteri* and *T*. cf. *winteri* from Bali in a clade (BI: 1.00, BS (ML): 97, BS (MP): 93). A sister group relationship of *T. amarula* and *T. winteri* was recovered in the BI and ML analyses (BI: 0.99, BS (ML): 83) but not in the MP analysis (BS (MP): < 50). Within this clade, the clades including specimens of *T. amarula*, *T. winteri*, and *T*. cf. *winteri* from Bali, respectively, were supported (BI: 1.00, BS (ML): 96–100, BS (MP): 100). The clade containing *T. amarula*, *T. winteri*, and *T*. cf. *winteri* was recovered as the sister group of a clade containing "*S*." *denisoniensis* and specimens from Thailand, Australia, and Indonesia (including also a single specimen from Bali) assigned to the *T. aspera* on basis of conchological similarity with rather high support (BI: 1.00, BS (ML): 92, BS (MP): 96). Within this clade, "*S*." *denisoniensis* was recovered as the sister group (BI: 1.00, BS (ML): 94, BS (MP): 90) of *T. aspera*, which in turn formed a rather well-supported clade (BI: 1.00, BS (ML): 90, BS (MP): 79). *Thiara aspera* specimens from Australia (Clade C) formed a maximally supported clade. The *T. aspera* specimens from Thailand grouped together with a single individual from Bali in a well-supported clade (Clade A; BI: 1.00, BS (ML): 92, BS (MP): 100), which was sister to another supported clade (Clade B; BI: 1.00, BS (ML): 77, BS (MP): 100) that included *T. aspera* specimens from Sulawesi.

The included specimens of *Mieniplotia scabra* (Müller, 1774) formed the sister clade of a specimen of *Melanoides tuberculata* from India in the BI analysis, albeit without support. To test alternative phylogenetic hypotheses, we conducted four AU tests: 1) the monophyly of *M. scabra* (p = 0.252) and 2) the monophyly of *T. winteri* plus the *T*. cf. *winteri* specimens from Bali ($p = 0.156$) could not be rejected, whereas 3) the monophyly of *T. aspera*, *T. winteri* and *T*. cf. *winteri* ($p < 0.001$) and 4) the monophyly of *Thiara* excl. "*S*." *denisoniensis* ($p = 0.033$) but including the *T. aspera* specimens was rejected at a confidence level of $\alpha = 0.05$.

Systematic account

Thiaridae Gill, 1871 (1823)

***Thiara* Röding, 1798**[*]

Vesica Humphrey, 1797: 58 [unavailable, published in a work rejected for nomenclatural purposes, see International Commission on Zoological Nomenclature 1912: 116–117; among the mentioned species is *Vesica thiara* Humphrey, 1797 (unavailable) = *Helix amarula* Linnaeus, 1758].

Thiara Röding, 1798: 109 [type species: *Helix amarula* Linnaeus, 1758, by subsequent designation of Herrmannsen 1849 in Herrmannsen 1847–1849: 576].

Melania Lamarck, 1799: 75 [type species: *Helix amarula* Linnaeus, 1758, by monotypy].

Melanigenus Renier, 1807: pl. 8 [unavailable, published in a work rejected for nomenclatural purposes, see International Commission on Zoological Nomenclature 1956: 290].

Melas Montfort, 1810: 322–324 [unjustified emendation of *Melania* Lamarck, 1799].

Melanidia Rafinesque, 1815: 144 [unjustified emendation of *Melania* Lamarck, 1799].

Melanea – Sowerby 1818 in Sowerby 1818–1822: 33 [incorrect subsequent spelling of *Melania* Lamarck, 1799].

? *Spirilla* Gray, 1824: 254 [unavailable, published in synonymy; mentioned as *Spirilla spinosa* (quoting a label or note attributed to G. Humphrey as "*Spirilla spinosa*, freshwater spiral spined shell, from Admirality Island, New Guinea") under *Melania setosa* Swainson, 1824 (= *Thiara cancellata* Röding, 1798, see Swainson 1824: 13–15 and Wilkins 1957: 167–169) and as being conspecific with the nomenclaturally unavailable *Buccinum aculeatum* Lister, 1692: pl. 1055, fig. 8. Mentioned as a synonym by Férussac 1824: 318, Gray 1825: 524, Oken 1833: 133, Gray 1847: 152, Wilkins 1957: 167 as well as by Agassiz 1842: 84, Agassiz 1847: 348 and Herrmannsen 1848 in Herrmannsen 1847–1849: 491 in nomenclators, with the name attributed to Humphrey 1797 (where it could not be found). Used by Favre 1869: 79 (attributing the name to G. Humphrey but without reference to the work of Gray 1824) for a subgenus of *Fusus* Bruguière 1789 in Bruguière 1789–1792 and in a very different meaning from that of Gray 1824 and therefore not regarded here as having been made available from that work].

Spirella – Oken 1833: 61 [incorrect subsequent spelling of the unavailable *Spirilla* Gray, 1824].

Melacantha Swainson, 1840: 341 [type species: *Helix amarula* Linnaeus, 1758 by subsequent designation of Herrmannsen 1849 in Herrmannsen 1847–1849: 26].

Thaira – Gray 1840: 148 [incorrect subsequent spelling of *Thiara* Röding, 1798].

Amarula Sowerby, 1842: 61 [type species: *Helix amarula* Linnaeus, 1758, by monotypy].

Melanium – Busch 1842 in Philippi 1842–1845: 4 [incorrect subsequent spelling of *Melania* Lamarck, 1799].

Tiara – Gray 1847: 152 [incorrect subsequent spelling of *Thiara* Röding, 1798].

Thaera – Agassiz 1847: 367 [unavailable, emendation for *Thaira* as used by Gray 1840: 148 proposed in synonymy in a nomenclator].

Lithoparches Gistel, 1848: ix [nom. nov. pro *Melania* Lamarck, 1799; type species: *Helix amarula* Linnaeus, 1758, by typification of the replaced name].

Hydrognoma Gistel, 1848: 169 [nom. nov. pro *Melania* Lamarck, 1799, type species: *Helix amarula* Linnaeus, 1758, by typefication of the replaced name].

Tiaropsis Brot, 1871: 298 [non Agassiz 1849: 289–298; type species: *Melania winteri* Busch, 1842 in Philippi 1842–1844: *Melania*, 1, pl. 1 figs 1, 2 by subsequent designation of Brot 1874 in Brot 1874–1879: 7].

Cerithomelania Moore, 1899: 233–234 [type species: *Helix amarula* Linnaeus, 1758 by original designation].

? *Ripalania* Iredale, 1943: 209 [type species: *Melania queenslandica* Smith, 1882 by monotypy].

? *Setaeara* Morrison, 1952: 8 [type species: *Thiara cancellata* Röding, 1798 by original designation].

[*] a question mark indicates a tentative synonymisation

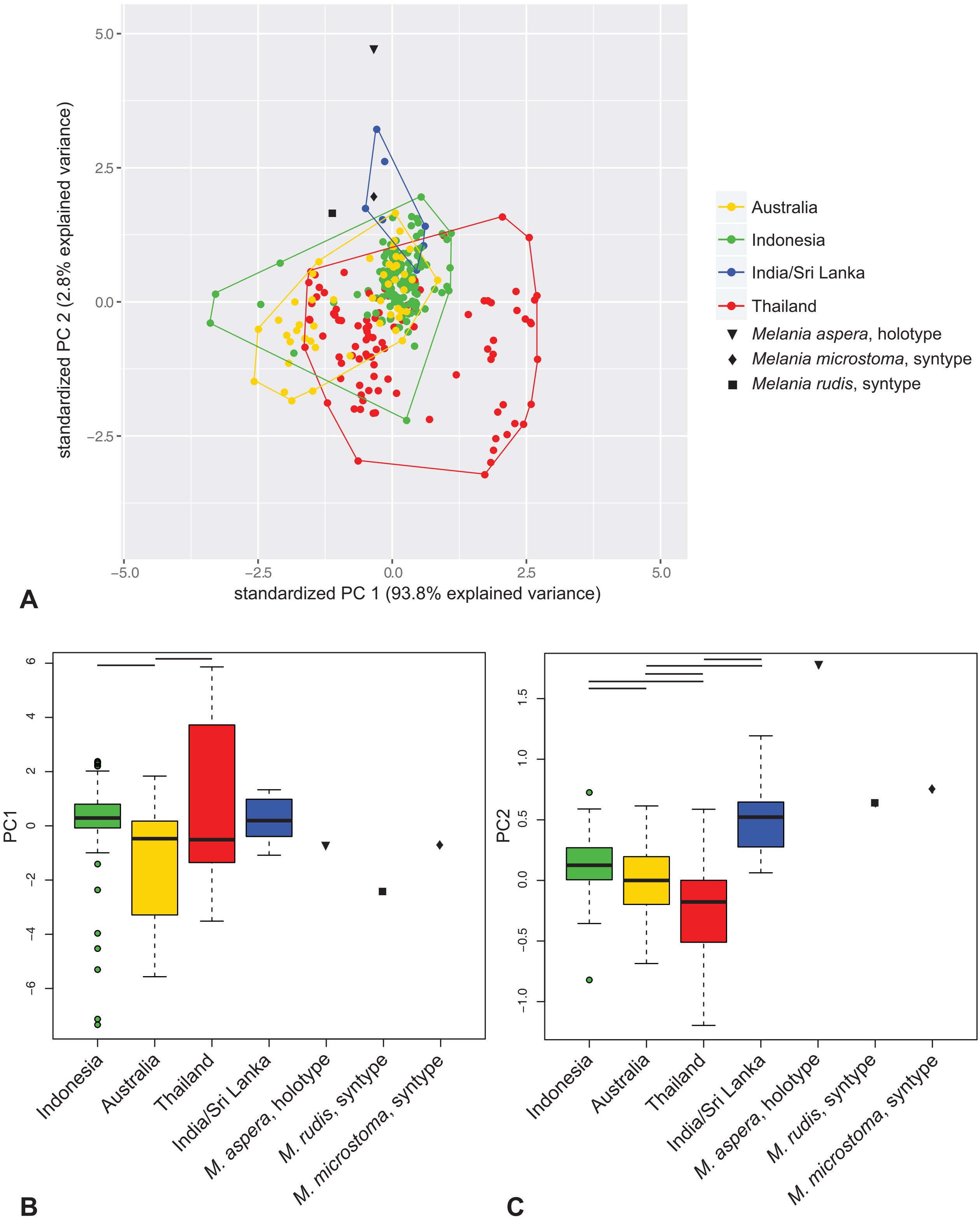

Figure 4. Results of the analysis of biometric data of "*Thiara*" *aspera* (Lesson, 1831) specimens from Australia (yellow), Indonesia (green), Thailand (red) and India/Sri Lanka (blue) and type material of *Melania aspera* Lesson, 1831 (holotype, triangle), *Melania rudis* Lea & Lea, 1851 (syntype, square) and *Melania microstoma* Lea & Lea, 1851 (syntype, diamond). **A.** Scatter plot of the first two axes of the principal component analysis (PCA) of biometric data. Coloured lines indicate the outline of the convex hull for each geographic group; **B, C.** Boxplots of PCA 1 (**B**) and PCA 2 (**C**); bars above the box plots indicate significant differences of groups resulting from testing with Dunn's test.

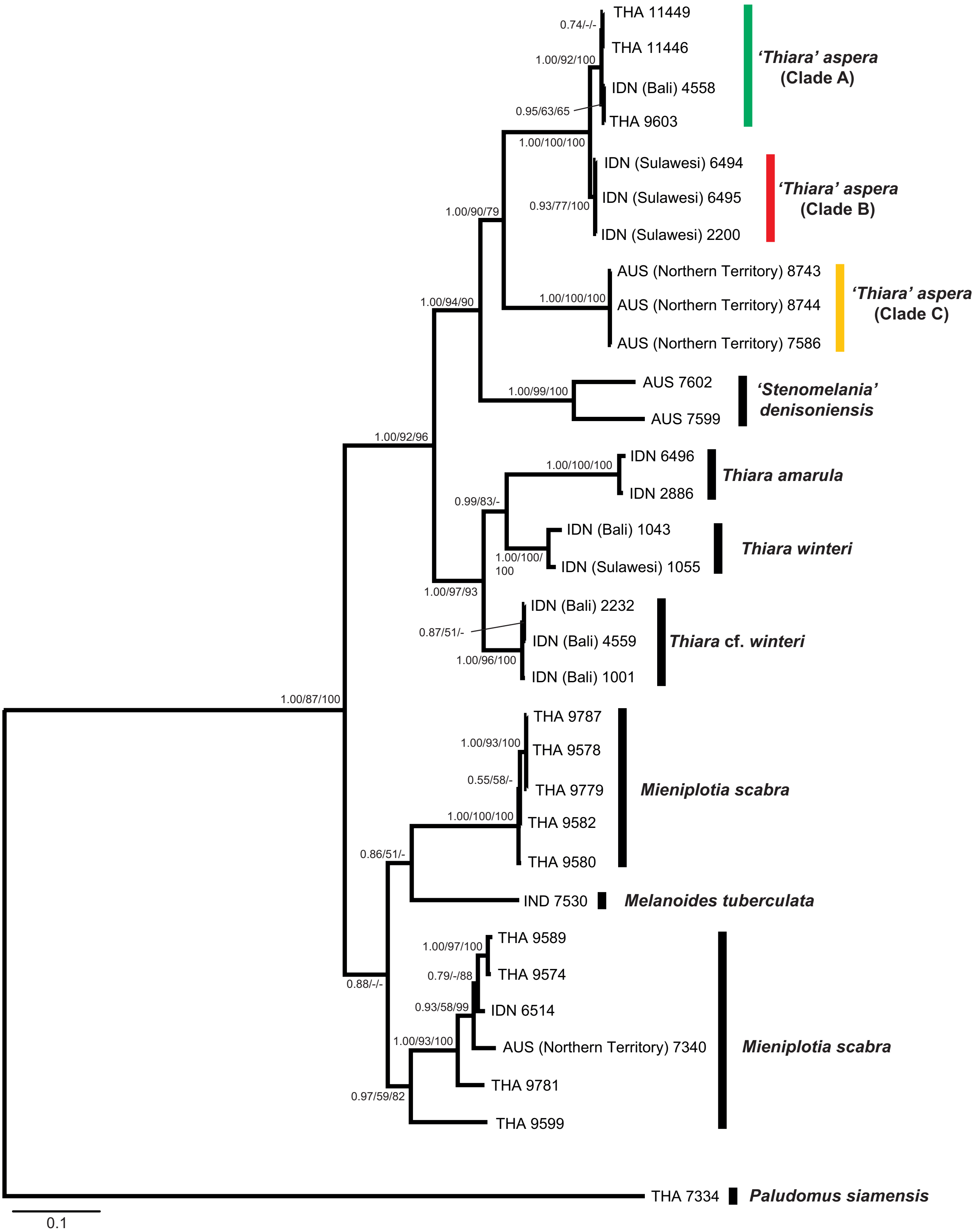

Figure 5. Bayesian 50% majority-rule consensus tree based on partial sequences mitochondrial cytochrome c oxidase subunit 1 (*cox1*) and 16S rRNA (16S) genes. Support values at nodes refer to Bayesian posterior probabilities (left), Maximum Likelihood (middle) and Maximum Parsimony (right) bootstrap values. AUS: Australia, IDN: Indonesia, THA: Thailand. Numbers at tips refer to DNA vouchers in the collection of the ZMB, see also Table 1.

Remarks. Many names have been proposed for the group of Thiaridae that is currently regarded as representing *Thiara* Röding, 1798. Several of these names are objective junior synonyms of *Thiara* having the same type species (*Helix amarula* Linnaeus, 1758), and several others are nomenclaturally unavailable. A few, like *Ripalania* Iredale, 1943 or *Setaeara* Morrison, 1952, may actually be synonyms of *Thiara*. However, those hypotheses should be further tested using molecular genetic approaches. Therefore, these nominal genera were only tentatively included in the synonymy of *Thiara*.

"*Thiara*" *aspera* (Lesson, 1831)*

Figs 1, 6, 7

Melania aspera Lesson, 1831 in Lesson (1830–1831: 357–358) [type locality: "La Nouvelle-Guinée" (= New Guinea), restricted to Manokwari by Glaubrecht and Podlacha (2010)].

Melania rudis Lea & Lea, 1851: 186 [type locality: 'Amboyna' (= Ambon)].

Melania microstoma Lea & Lea, 1851: 186 [type locality: mountain streams, isle of Negros, Philippines].

? *Melania armillata* Lea & Lea, 1851: 195–196 [type locality: India].

? *Melania broti* Reeve, 1859 in Reeve (1859–1861: pl. 22 fig. 160) [type locality: Ceylon (= Sri Lanka)].

? *Melania hybrida* Reeve, 1859 in Reeve (1859–1861: pl. 13 fig. 163) [type locality: not given].

? *Melania chocolatum* Brot, 1860: 256–257, pl. 16, fig 2 [type locality: "Ceylon" (= Sri Lanka)].

? *Melania* (*Tiaropsis*) *rudis* var. *spinosa* Brot, 1877 in Brot (1874–1879: 306) [type locality: not given, see also Brot (1868: 33, pl. 1, fig. 7)].

? *Melania* (*Tiaropsis*) *drilliiformis* Martens, 1897: 305 [nomen nudum].

? *Melania fortitudinis* Fulton, 1904: 51–52, pl. 4, fig. 3 [type locality: "Soekaboemi, Java" (= Sukabumi, Java)].

? *Melania rudis* var. *cylindrica* Schepman, 1915: 27 [type locality: West Ceram, Kairatu (= West Seram Island, Kairatu)].

Diagnosis. Thiarid with a turreted, subcylindrical to elongate-ovoid, strongly ornamented high-spired shell with usually rather flattened whorls and a narrowly pyriform aperture that at most reaches half the total shell height, but usually less. Ornamentation of the shell consisting of sinuous axial ribs that usually reach to the base of the body whorl and spiral chords that form nodes where they intersect the ribs; spiral chords usually present on the entire whorl but strongest at the base of body whorl.

Remarks. The examined type specimens of *M. aspera*, *M. rudis*, and *M. microstoma* correspond well to each other in overall shell shape and sculpture and are here regarded as conspecific because of this. As already noted by Brot (1874–1879: 307) and Glaubrecht and Podlacha (2010: 200), the name *Melania aspera* Lesson, 1830 has priority over the somewhat more frequently used name *Melania rudis* (e.g., van Benthem Jutting 1937, 1956; Subba Rao 1989; Ramakrishna and Dey 2007; Budha 2010; Patil and Talmale 2011 as *T. rudis*). The holotype of *Melania aspera* is unusual in possessing a very small aperture in relation to overall shell height, possibly explaining its isolated position in the PCA 1 vs PCA 2 scatter plot (Fig. 4A). The nominal taxa *M. armillata*, *M. broti*, and *M. chocolatum* described from India or Sri Lanka were regarded by Brot (1874–1879) as closely related to *M. rudis* and are here tentatively synonymised with *M. aspera*, largely following the views of Rensch (1934) and van Benthem Jutting (1937, 1956) who synonymised these taxa with *M. rudis*. According to Brot (1874–1879: 307–308) *Melania hybrida* is based on a teratological specimen with an unusual aperture formation and is here tentatively synonymised with *M. aspera*. The nominal taxon *Melania* (*Tiaropsis*) *rudis* var. *spinosa* Brot, 1877 is an individual variation of *M. aspera* with somewhat longer shoulder spines. The original figures and descriptions of *Melania fortitudinis* and *M.* (*Tiaropsis*) *rudis* var. *cylindrica* from Java and West Seram Island also correspond well with the holotype of *M. aspera* and are herein treated as synonyms of the former.

Type material examined. Holotype of *Melania aspera* Lesson, 1831, MNHN 21098, "La Nouvelle-Guinée"; syntype of *Melania rudis* Lea & Lea, 1851, USNM 119778, "Amboyna"; syntype of *Melania microstoma* Lea & Lea, 1851, USNM 119722, 'mountain streams, isle of Negros, Philippines'.

Additional material examined (w: ethanol preserved samples). **India**: Kolkata, ZMB 107002. **Sri Lanka**: Colombo, ZMB 107003. **Thailand**: Samut Sakhon Province, Klong Don Ko, SUT 0311020, ZMB 127535, SUT 0311044, SUT 0311053, ZMB 127534, w; Nakhon Pathom province, Pond in Silpakorn University campus, SUT 0312069, SUT 0312070 = ZMB 127536, w. **Indonesia**: Bali: South Bali, Yehembang River, ZMB 191279, ZMB 191279a, w, South Bali, at Yehembang, ZMB 106472, w; east of Mendaya, stream southwest of Gumicik, ZMB 191488; Sulawesi: South Sulawesi, Kalena catchment, Angkona river, ZMB 192751, w; southeast Sulawesi, Pohara river, at Pohara, road Kendair to Kolaka, ZMB 191261, w; southeast Sulawesi, Simbune river, 1 km northeast of Raterate, road Kendari to Kolaka, ZMB 191262, ZMB 191262a, w; southeast Sulawesi, stream at Tembeeha, road Tirobus to Kendari, ZMB 191278, w; central Sulawesi, Banggai Islands, Peleng Island, West Peninsula, Tataban river, ZMB 107378, w, ZMB 107377,w. **Australia**: Northern Territory: Berry Springs, ZMB 106704, w, ZMB 106599a, w, ZMB 127616, w; Wabalaar, Roper River, ZMB 107617, w, ZMB 107614, w, ZMB 127645, w; Salt creek, ZMB 127619, w, ZMB 127636, w, ZMB 127637, w; Roper Bar, ZMB 127620, w; Queensland: O'Shanassy, ZMB 107280.

* a question mark indicates a tentative synonymisation

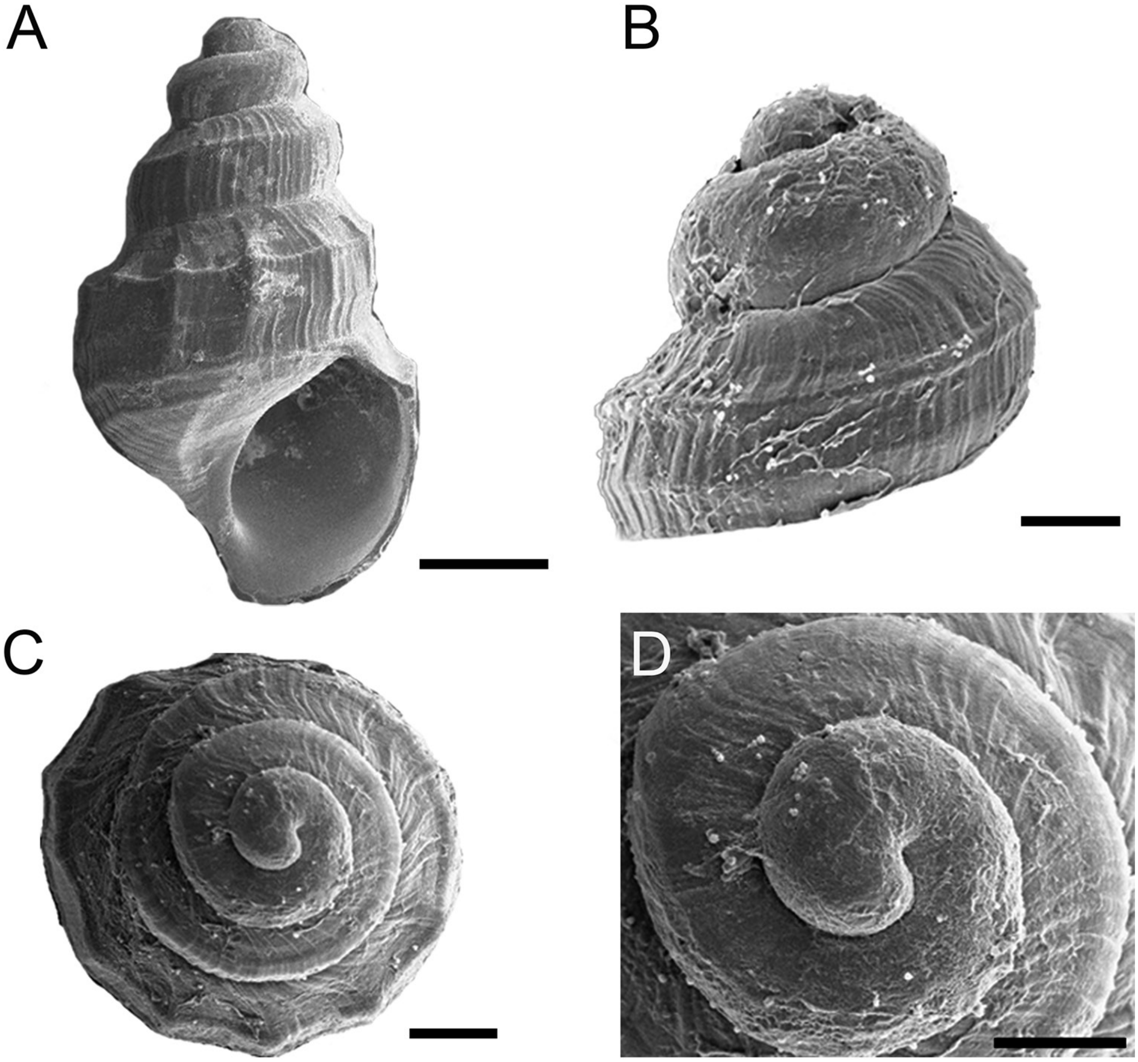

Figure 6. Juvenile and embryonic shells of "*Thiara*" *aspera* (Lesson, 1831), SUT 0311020, Samut Sakhon Province, Klong Don Ko. **A.** Lateral view; **B.** Apical whorls, lateral, **C.** Apical view. **D.** Details of the protoconch. Scale bars: 450 µm (**A**); 250 µm (**B**); 200 µm (**C**); 100 µm (**D**).

Shell. Turreted, subcylindrical to elongate-ovoid, corneous to dark brown, with up to nine whorls (the early whorls usually eroded) (Fig. 1; for juvenile shells, see Fig. 6). Whorls rather flat to convex, separated by a slightly impressed to distinctly impressed, undulating suture. Whorls slightly constricted below the suture, ornamented with sinuous ribs and spiral chords that usually form nodules at their intersections. Radial sculpture usually strongest on the upper half of the whorls, with the nodules at the shoulder of the whorls usually largest, sometimes forming spines. Towards the lower part of the body whorl the spiral sculpture often becomes the dominant sculptural element, forming distinct parallel chords. Aperture pyriform, angled in its upper part and rather narrow, wider at the base and appearing truncated in frontal view. Columella thickened, almost straight to curved, abruptly terminating basally. Shell size H = 7.6–48.0 mm, W = 3.1–22.0 mm (Table 2).

Operculum. The operculum is typical for thiarids, oval and paucispiral, light to dark brown, and with the nucleus being excentric in the lower left corner.

Juvenile shell. The shells of the juveniles in the brood pouch had up to five whorls, with a maximum height of about 2.5 mm. The protoconch is smooth, with the radial and spiral sculpture developing on the first teleoconch whorls (Fig. 6). For measurements of the embryonic shell, see Table 3.

Radula. Taenioglossate (Fig. 7), resembling other thiarids. As in all thiarids the central tooth or rachidian is significantly wider than tall; all specimens have a central cusp flanked by three to six triangular denticles on both sides, resulting in up to 12 denticles and a typically 4–5/1/4–5 pattern at the upper cutting edge (Fig. 7A, C, E, Table 4). The laterals are equipped with three to six

Table 2. Shell parameters of "*Thiara*" *aspera* (Lesson, 1831) specimens from Thailand, Indonesia and Australia, with min./max. values, mean, standard deviation (SD), and number of whorls.

Voucher	Country, region	*n*		Measurements (mm)					NW
				H	W	AL	AW	BW	
USNM 119778	Indonesia, Ambon Island	1		23.7	9.7	9.8	5.1	15.5	4
USNM 119722	Philippines, Negros Island	1		20.3	7.7	7.1	3.3	12.3	6
MNHN 21098	Indonesia, West Papua	1		25.0	7.8	6.9	3.5	12.6	7
GSUBg 14265	Indonesia, Java	1		48.0	22.0	22.0	10.0	28.1	7
ZMB 107002	India, Calcutta	1		17.4	7.5	5.7	2.5	12.0	3
ZMB 107003	Sri Lanka, Colombo	5	Range	13.3–16.6	5.3–6.6	4.3–5.3	2.3–2.5	9.0–11.3	4–5
			Mean	14.3	5.9	4.8	2.4	9.8	
			SD	1.2	0.4	0.3	0.1	0.8	
SUT 0311053	Thailand, Samut Sakhon	30	Range	7.6–12.8	3.1–5.5	2.8–6.2	1.6–3.4	4.4–7.8	4–7
			Mean	9.5	3.9	4.0	2.3	5.7	
			SD	1.1	0.6	0.6	0.4	0.9	
SUT 0311020	Thailand, Samut Sakhon	52	Range	14.1–24.3	7.1–11.1	7.0–11.1	3.2–5.4	9.7–16.2	6–7
			Mean	17.7	8.7	8.7	4.2	12.0	
			SD	2.5	1.0	1.0	0.5	1.5	
SUT 0311044	Thailand, Samut Sakhon	1		22.9	10.9	10.5	4.8	15.2	6
SUT 0312070	Thailand, Nakhon Pathom	12	Range	14.4–19.8	5.3–7.9	5.7–6.8	2.4–4.2	7.6–12.0	5–8
			Mean	17.1	6.8	7.0	3.4	9.9	
			SD	1.5	0.7	0.9	0.5	1.2	
ZMB 191488	Indonesia, Bali	2	Range	19.8–22.1	8.3–9.4	8.0–8.8	4.1–4.7	12.8–14.5	5
			Mean	20.9	8.9	8.4	4.4	13.7	
			SD	1.1	0.6	0.4	0.3	0.9	
ZMB 191278	Indonesia, Sulawesi	19	Range	14.3–18.2	6.2–7.8	6.1–8.9	3.1–3.9	9.3–12.3	4–5
			Mean	16.1	6.7	7.2	3.6	10.4	
			SD	1.0	0.3	0.6	0.2	0.7	
ZMB 107377	Indonesia, Sulawesi	10	Range	13.6–20.3	5.5–7.5	4.5–7.3	2.7–4.0	7.7–11.7	4–5
			Mean	16.8	6.5	6.2	3.4	9.6	
			SD	2.1	0.7	0.8	0.4	1.3	
ZMB 107378	Indonesia, Sulawesi	19	Range	12.9–19.6	5.2–7.1	5.1–7.8	2.6–3.9	7.7–11.2	4–5
			Mean	16.9	6.3	6.3	3.2	9.9	
			SD	1.5	0.4	0.7	0.4	0.8	
ZMB 191279	Indonesia, Bali	17	Range	16.8–27.0	7.0–9.9	7.9–12.0	3.3–5.1	11.0–17.2	4–6
			Mean	22.7	8.6	9.9	4.3	14.5	
			SD	3.7	1.0	1.4	0.6	2.2	
ZMB 106472	Indonesia, Bali	16	Range	17.9–22.8	6.4–9.3	7.0–10.6	3.1–5.0	11.4–16.2	4–7
			Mean	20.1	7.5	8.5	3.8	12.7	
			SD	1.4	0.6	0.9	0.4	1.2	
ZMB 127538	Indonesia, Bali	20	Range	18.4–30.4	8.6–13.7	9.3–14.9	4.4–7.4	12.8–20.7	4–6
			Mean	24.8	11.0	11.8	5.6	16.8	
			SD	3.0	1.2	1.4	0.7	1.9	
ZMB 191268	Indonesia, Sulawesi	5	Range	29.3–41.5	11.5–16.0	12.1–18.7	5.7–8.4	12.3–26.8	4–6
			Mean	35.3	13.5	15.3	6.9	20.9	
			SD	4.9	2.0	2.5	1.1	5.3	

Table 3. Measurements of parameters of the juvenile protoconch of "*Thiara*" *aspera* (Lesson, 1831) of specimens obtained from the brood pouch.

Voucher	Country, region	*n*		Measurements (µm)		
				he	we	de
ZMB 127534	Thailand, Samut Sakhon	3	Range	48.0–63.2	96.0–120.0	312.7–395.7
			Mean	54.0	106.7	352.8
ZMB 127535	Thailand, Samut Sakhon	2	Range	56.3–71.4	107.0–114.3	354.3–366.2
			Mean	63.9	110.7	352.8
ZMB 191278	Indonesia, Sulawesi	2	Range	34.0–72.4	76.0–91.1	202.0–252.4
			Mean	53.2	84.6	227.2
ZMB 191488	Indonesia, Bali	1	–	83.3	95.2	259.5

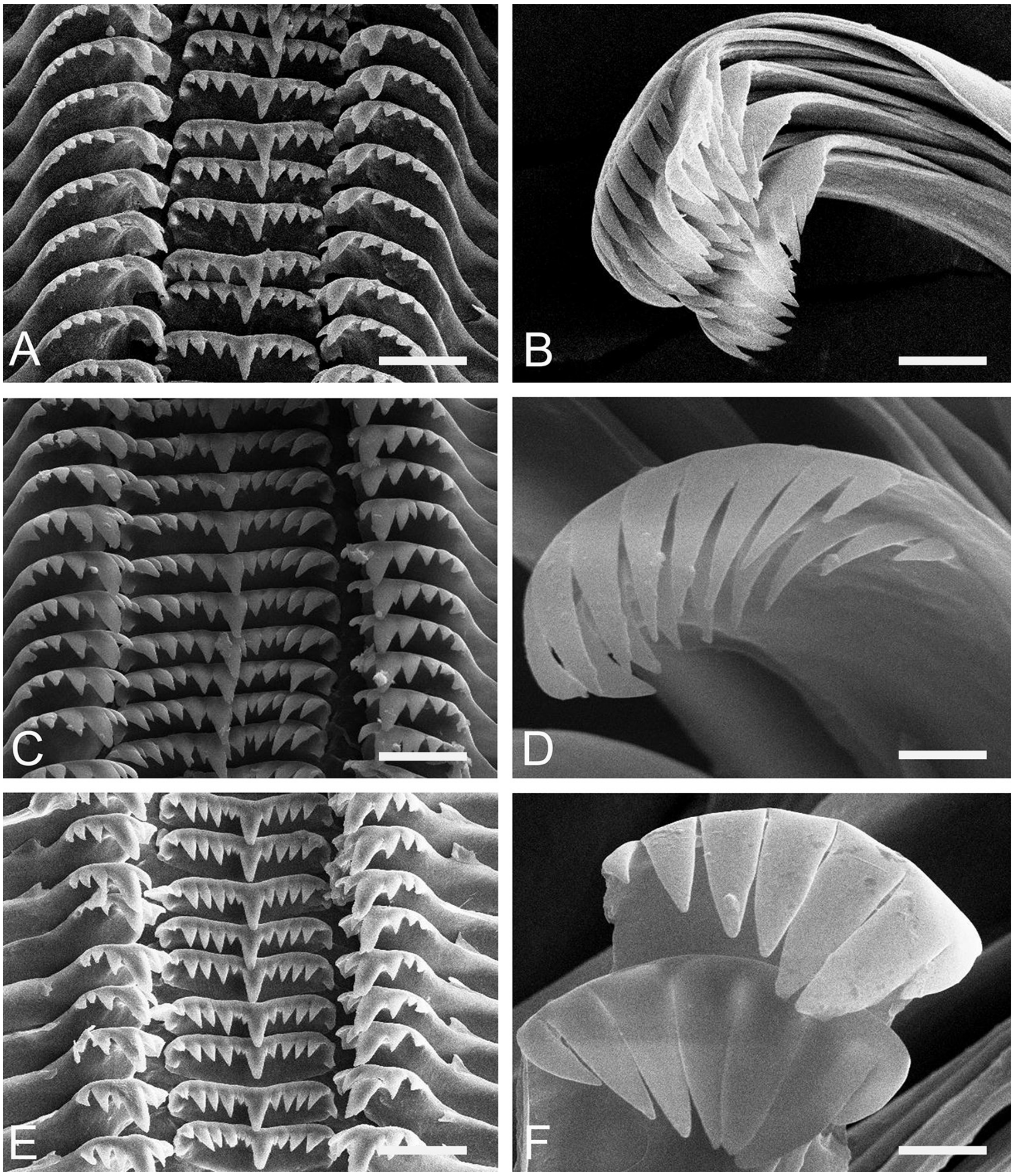

Figure 7. Radulae of "*Thiara*" *aspera* (Lesson, 1831) from Thailand. **A, B.** SUT 0312070, Nakhon Pathom province, pond at Silpakorn University campus; **A.** Central and lateral teeth; **B.** Marginal teeth; **C, D.** SUT 0311020, Samut Sakhon province, Klong Don Ko; **C.** Central and lateral teeth; **D.** Marginal teeth. **E, F:** SUT 0311053, Samut Sakhon Province, Klong Don Ko; **E.** Central and lateral teeth; **F.** Marginal teeth. Scale bars: 35 µm (**A, E**); 5 µm (**B, F**); 25 µm (**C**); 10 µm (**D**).

Table 4. Variation of cusps on the radula teeth of "*Thiara*" *aspera* (Lesson, 1831) specimens.

Voucher	Country, region	*n*	Marginal teeth	Lateral teeth (left)	Lateral teeth (right)	Rachidian
SUT 0311053	Thailand, Samut Sakhon	4	6–8	3·1·3	3·1·3	4–5·1·4–5
SUT 0311020	Thailand, Samut Sakhon	4	6–8	3·1·3	3·1·3	4–5·1·4–5
SUT 0312070	Thailand, Nakhon Pathom	2	7–8	5·1·5	4·1·4	4·1·4
SUT 0312069	Thailand, Nakhon Pathom	2	9–10	3·1·3	3·1·3	3·1·3
ZMB 191278	Indonesia, Sulawesi	2	7–8	3·1·3	3·1·3	4·1·4
ZMB 191488	Indonesia, Bali	1	10	6·1·6	6·1·6	6·1·5
ZMB 191279	Indonesia, Bali	3	6–7	4·1·4	4·1·4	4–5·1·4–5
ZMB 106472	Indonesia, Bali	2	6–7	3·1·3	3·1·3	4·1·4

smaller denticles on the inner side, and three to six denticles outside from the large main cusps (Fig. 7A, C, E, Table 4). The marginal teeth are moderately long, spoon-shaped, with a varying number of 6–10 denticles (Fig. 7B, D, F, Table 4).

Reproductive strategy. The results of the analysis of brood pouch content are summarised in Figure 2. Juveniles of up to 2 mm (rarely also larger) were found in the populations from Thailand, Indonesia (Bali and Sulawesi) and Australia (Northern Territory) suggesting an euviviparous reproductive strategy for "*T.*" *aspera*, i.e, the taxon was found to give birth to crawling and shelled juveniles in accordance with the definitions in Glaubrecht et al. (2009). In a few populations in Thailand and on Bali, gravid females with only early embryos, i.e., veliger larvae in the brood pouch were found.

Distribution. "*Thiara*" *aspera* as here understood is a widespread species, with records from Sri Lanka and India (Subba Rao 1989), Myanmar and Cambodia (van Benthem Jutting 1956), Indonesia (Rensch 1934; van Benthem Jutting 1956), and the Philippines (Lea and Lea 1851; van Benthem Jutting 1956). As our results indicate, the taxon is also present in Thailand and northern Australia, from where it was not previously reported (Fig. 2).

Discussion

The results of our phylogenetic analyses show that the nominal taxon *Melania winteri* Busch, 1842 is closely related to *Thiara amarula* and can be classified with the same genus. However, the nominal species *Melania aspera* Lesson, 1830 (= *Melania rudis* Lea & Lea, 1851), which has often been classified as a member of *Thiara* (e.g., van Benthem Jutting 1937, 1956; Subba Rao 1989; Ramakrishna and Dey 2007; Budha 2010; Patil and Talmale 2011 under the name *T. rudis*) cannot be included within that genus on the basis of our data without broadening the concept of *Thiara* to an extent that it encompasses almost the entire conchological diversity of Thiaridae because "*Stenomelania*" *denisoniensis* Brot, 1877, which is conchologically similar to *Stenomelania* Fischer, 1885 or *Melanoides* Olivier, 1804, clusters within *Thiara* s. lat. in our phylogenetic analyses and an approximately unbiased test rejected the monophyly of *T. amarula*, *T. winteri*, T. cf. *winteri*, and "*T*". *aspera*, i.e., excluding "*Stenomelania*" *denisoniensis*. Pending a phylogenetic analysis of the entire family, we here retain the species in *Thiara*, but indicate the tentative placement by quotation marks.

Our phylogenetic analyses further show that "*T.*" *aspera* exhibits little genetic variation throughout the Indo-Malayan Archipelago and the Southeast Asian mainland, although populations vary considerably with regard to shell shape, and especially sculpture, confirming previous surveys on thiarid species, which showed also an extraordinary plasticity of the shell (Glaubrecht et al. 2009). We here report the presence of "*T.*" *aspera* in Thailand for the first time, albeit in anthropogenic habitats. Previous surveys of the Thai freshwater snail fauna, e.g., by Brandt (1974) did not record the species. Thus, as his years-long surveys were exhaustive it is safe to assume that the species is probably introduced but additional surveys should be carried out to clarify whether the taxon also occurs in natural habitats in this country and was only overlooked in the past.

We also report "*T.*" *aspera* here for Australia for the first time, where the taxon was found in natural habitats in the Northern Territory and in north-western Queensland. The populations from Australia were found to be somewhat differentiated genetically from the remaining specimens of "*T.*" *aspera* from Thailand and Indonesia included in the phylogenetic analyses and also slightly differ conchologically, i.e., the spiral sculpture almost disappears on the upper half of the teleoconch whorls. Further analysis should therefore confirm whether these differences are constant and would allow a taxonomic separation of the Australian populations.

Unfortunately, no samples could be included in the phylogenetic analyses from either India or Sri Lanka. However, as the examined material closely resembles the holotype of *Melania aspera* in shell characters (although this specimen is exceptional because of its very small aperture in relation to total shell height which may explain its isolate position in Fig. 4A), the populations from these two countries are here regarded as belonging to the species. Therefore, "*T.*" *aspera* has to be considered as a widespread species, ranging from India and Sri Lanka across the Southeast Asian mainland and islands into Australia (Fig. 2).

At present, our data on "*T.*" *aspera* do not allow to assess whether the observed differences of juvenile stages in the brood pouch of the female indicate differences in the reproductive strategy, or rather individual or seasonal variations. The close phylogenetic relationships among these populations (Fig. 5), however, let the latter two explanations appear more likely in our opinion. Therefore, we consider "*T.*" *aspera* a euviviparous species, although it has to be stated that repeated periodic sampling would be necessary to resolve this issue conclusively.

Conclusions

These results highlight the need for a comprehensive revision of the genus-group systematics of Thiaridae as a whole. However, mitochondrial DNA markers are fraud with difficulties in some freshwater cerithioideans (Köhler and Deein 2010; Whelan and Strong 2015; Köhler 2016) and probably also in Thiaridae. Likewise, there appears to be a confusing variability in shell and reproductive features in thiarids, which is in stark contrast to a conserved radular morphology as compared to some other cerithioidean families (Glaubrecht 1996). A stable system of the family, which ought to include the type species of all named genus-group taxa, can be expected to emerge only after phylogenetic analyses based on suitable molecular markers and/or detailed morphological data become available. A stable system of the family then could serve as a basis for a better understanding of the evolutionary systematics and phylogeography of the group.

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