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CLARIFICATION OF THE TAXONOMIC STATUS OF *PAPHIA MALABARICA* (CHEMNITZ, 1782) AND DOES IT MATTER?

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Abstract: The short neck clam, which forms the major resource of Ashtamudi Lake, Kerala, India is economically very significant and the fishery has gained India's first Marine Stewardship Council (MSC) certification. All published reports hitherto from the Ashtamudi Lake recorded the short-neck clam as *Paphia malabarica* (Dillwyn, 1817) now synonymised with *Protapes gallus* (Gmelin, 1791). Recently, the true taxonomic identity of the Ashtamudi short neck clam was revealed as *Marcia recens* (Holten, 1802) by conventional taxonomic studies. The present paper uses molecular techniques to validate the taxonomic position of Ashtamudi short-neck clam and substantiates the taxonomic positioning of Ashtamudi short-neck clam under the genus *Marcia*.

Key words: *Protapes gallus*, Ashtamudi Lake, MSC Certification, Molecular taxonomy, *Marcia recens*

INTRODUCTION

The Ashtamudi Lake short-neck clam (Fig.1) is the major economically valuable fishery resource of the brackish water Ashtamudi Lake in Kerala, India which carries a Marine Stewardship Council (MSC) certification for sustainability. Arathi *et al*. (2018) proposed that the short-neck clam that forms a major fishery in Kerala, southwest coast of India should be correctly identified as *Marcia recens* (Holten, 1802). They gave nomenclatural and morphological reasons why the name *Paphia malabarica* was both unavailable and inappropriate. Sukumaran *et al*. (2019) refuted the findings of the above paper and proposed to retain the name *Paphia malabarica* (Chemnitz, 1782) for the short-neck clam.

Here we explain why the specific epithet is not available and why the generic placement in *Paphia* contradicts the current systematics of the Veneridae. We state now that we are in agreement with Sukumaran *et al*. (2019) in recognising that the short-neck clam is not *Protapes gallus* (Gmelin, 1791) but we cannot condone the lack of conformity with the rules of nomenclature in suggesting the retention of the name *Paphia malabarica* (Chemnitz, 1782).

This debate brings into focus the role of taxonomy in fisheries biology and does the correct taxonomy matter?

Nomenclature

Paphia malabarica is based on *Venus malabarica* Chemnitz, 1782. The name *malabarica* Chemnitz, 1782 is not available because it was published in Martini & Chemnitz 1769-1795 Neues Systemarisches Conchylien-Cabinet, volumes 1-11. This work was deemed unavailable for nomenclatural purposes because the authors did not apply the principles of binomial nomenclature (Melville and Smith, 1987).

The name *malabarica* was subsequently made available by Dillwyn, 1817 but had already been placed into synonymy with *Venus gallus* Gmelin 1791. Both Gmelin (1791) and Dillwyn (1817) indicate that they consider their taxa to be that

described and illustrated as *Venus malabarica* Chemnitz, 1782. Consequently, all three taxa are based on the same concept, *ie* they have the same name bearing type which in this case are the illustrations in Chemnitz (1782: figs 324, 325). While the names *V. malabarica* and *V. gallus* share the same name bearing type, that type specimen cannot represent more than one species. Consequently the names *malabarica* and *gallus* cannot be used for different species.

In accepting the species *Protapes gallus* Sukumaran *et al*. (2019) cannot then use the name *P. malabarica* for a different species. Current nomenclature such as that adopted by MolluscaBase (2019), Subba Rao (2017) and Huber (2010) all accept that *Venus malabarica* of Chemnitz and authors is synonymous with *Protapes gallus* (Gmelin, 1791). We agree with Sukumaran *et al.* (2019) that the short-neck clam is not *Protapes gallus* and thereby the short-neck clam cannot take the name *malabarica* of any author.

Generic placement

Sukumaran *et al*. (2019) gave molecular and morphological reasons why the Ashtamudi short-neck clam was not *Paphia* (*Protapes*) *gallus* and we agree that this is correct. However, in attempting to give a generic placement Sukumartan *et al.* (2019) present a molecular tree consisting entirely of species belonging to the genus *Paphia*, no other Tapetinae were included so no sequences from *Marcia*, *Tapes*, *Ruditapes*, and *Protapes* were used despite them being available from studies such as Chen *et al*. (2011, 2014a,b). Sukumaran *et al*. (2019) state that they included species of *Marcia* and *Ruditapes* in their molecular analysis but none of the species indicated fall into these genera. A consequence of this is that the Short-neck clam must fall into their *Paphia* group as no others are considered.

Furthermore, they dismiss the morphological differences between currently accepted genera quoting Mikkelsen *et al*.(2006) and giving ecophenotypic variation as a reason not to explore the genera further. Arathi *et al*. (2018) illustrated considerable variation in the short-neck clam but in significant characters such as the orientation of the pallial sinus, there was no variation and consistently different in orientation from *Protapes gallus* and species of *Paphia*. In *Paphia* [as illustrated here from the type species *Paphia rotundata* (L. 1758)] and *Protapes* [as illustrated here from the type species *Protapes gallus* (Gm. 1791)] the pallial sinus rises steeply from the pallial line (Fig. 2 & 3). In contrast in *Marcia*, including the type species (*Marcia opima* (Gm. 1791), the pallial sinus is orientated almost parallel to the pallial line (Fig. 2F; 3 D). Other consistent differences in morphology include the excavated lunule margin and subtruncate posterior ventral margin seen in *Protapes* species but not in *Marcia* (Fig. 2 & 3). In both *Paphia* and *Protapes* the sculpture is of commarginal regular ridges but in *Marcia* the sculpure is finer from smooth (in *M. opima*) to irregularly sized lines and weak ridges in *M. recens* (Fig. 2 & 3). Subba Rao (2017) whose seminal work which recognises *Marcia*, *Paphia* and *Protapes* was not considered by Sukumaran *et al*. (2019). Using the keys given by Subba Rao (2017) the shortneck clam keys out as *Marcia recens* not *Paphia* or *Protapes*. Earlier papers (Melvill & Abercrombie, 1893) cite the presence of *Venus marmorata* Lamarck, 1818 from Mumbai (Bombay) but from these are *M. recens* (Fig. 2). Currently WoRMS (2019) and MolluscaBase (2019) recognise tapetinid genera and are defined by Huber (2010). Mikkelesen *et al*. (2006) discusses the mismatch between morphology and molecular trees, that is the relationships of the genera to each other but do not conclude that the majority of the genera are poorly defined.

Consequently, we reiterate the conclusions of Arathi *et al.* (2018) in stating that the morphology of the Ashtamudi clam is entirely consistent with the species

Fig. 1. Ashtamudi Lake Short Neck Clam *Marcia recens*

Marcia recens (Holten, 1802) and that the orientation of the pallial sinus and the external sculpture pattern are different from any recognised species of *Paphia* or *Protapes,* giving molecular evidences.

MATERIALS AND METHODS

A total of 24 venerid clam tissue samples were barcoded which includes *M. recens* (collected from Ashtamudi Lake and also from its type locality, Tuticorin), its congener and sympatric species in Ashtamudi lake, *M. opima*, *Protapes gallus* (=*Paphia malabarica*) from coastal waters of Kannur and its congener *P. ziczac* from Kollam coast. Seventeen samples were of *Marcia recens*, 3 samples were of *Protapes gallus* (=*Paphia malabarica*), and 2 samples each were of *M. opima* and *P. ziczac*. Adductor muscle tissue preserved in absolute alcohol was used for isolation of genomic DNA using QiagenDNeasy Tissue kit (Qiagen, Hilden, Germany) following the manufacturer's guidelines. DNA barcoding of specimen was carried out by sequencing the partial mitochondrial gene cytochrome oxidase 1 gene fragment, which is the extensively and successfully used gene in molluscan systematics. Gene amplification was done by using the primer set LCO1490 (5'-GGTCAACAAATCATAAAGATA TTGG-3') and HC02198 (5'-TAAACTTCA GGGTGACCAAAAATCA-3') (Folmer *et al*., 1994). Polymerase chain reactions were conducted with a total reaction volume of 25 µl consisting of 0.3 µl of each primer, 9.9 µl of double distilled water, 12.5 µl of Taq PCR master mix (QIAGEN, Hilden, Germany) and 2 µl of diluted DNA solution in an Eppendorf (Hamburg, Germany) thermal cycler. The PCR products were visualized on 1.5% agarose gels and the most intense products were selected for sequencing. PCR products were purified with USB ExoSAP-IT (Affymetrix Inc., Santa Clara, USA) and were sent for Sanger sequencing to Rajiv Gandhi Centre for Biotechnology**,** Thiruvananthapuram, India (www.rgcb.res.in). Sequence chromatograms were visualised and edited in Bioedit (Hall, 1999).

To assess the generic affinity of the Cytochrome Oxidase 1 (COX1) sequences generated for the Sukumaran *et al.* (2019) paper and the sequences generated during this study, we used a family wide multiple sequence alignment to construct a phylogenetic tree. First all 'Veneridae' COX1 sequences were searched in the NCBI GenBank and their accession numbers were downloaded. From among all the accession numbers (of Veneridae) the 'longest' COX1 sequences for a species was extracted. These sequences were downloaded, in fasta format, and used for further analysis. GenBank searches and downloads were carried out in R (R Core Team, 2014) computing environment using *AnnotationBustR* (Borstein and O'Meara, 2018). GenBank sequences MH730128-MH730158 (from the Sukumaran *et al.*, 2019 paper), the downloaded Venerid sequences and the sequences generated as part of this study were put together to create a multiple sequence alignment, initially the sequences were renamed (to make the header lines shorter and legible). A multiple sequence alignment of the dataset was carried out in SEAVIEW (Gouy *et al.*, 2009) using the MUSCLE algorithm (Edgar, 2004).

Raw genetic distances of selected sequences were computed using the *APE* package in R v.3.4 (Paradis *et al*., 2004; R core Team, 2014). Genetic distances were computed primarily to check if the Ashtamudi clam sequences were genetically similar to the topotypic *Marcia recens* sequences (collected from Tuticorin).

Maximum likelihood phylogeny was prepared using the IQTREE software (Nguyen, 2015). Initially the best partitioning (based on codon positions) and nucleotide substitution model was chosen using the model finder module of the IQTREE software (Nguyen, 2015). The best fit partitioning scheme and substitution model was used for phylogenetic analysis and an ultrafast bootstrap of 1000 replicates (Hoang *et al*., 2017) and 1000 shLRT replicates were used to assess the confidence at nodes of the phylogeny. The best tree was visualised using the FigTree v.1.4.3 software (Rambaut, 2017).

RESULTS AND DISCUSSION

NCBI GenBank has a total of 2398 Veneridae COX1 sequences (on 19th of December 2019), our search for the unique species yielded 152 sequences (most of them unique species). This data was added to the dataset of Sukumaran *et al.* (2019), MH730128-MH730158, which they claim to be *Paphia malabarica*, and with the sequences generated during

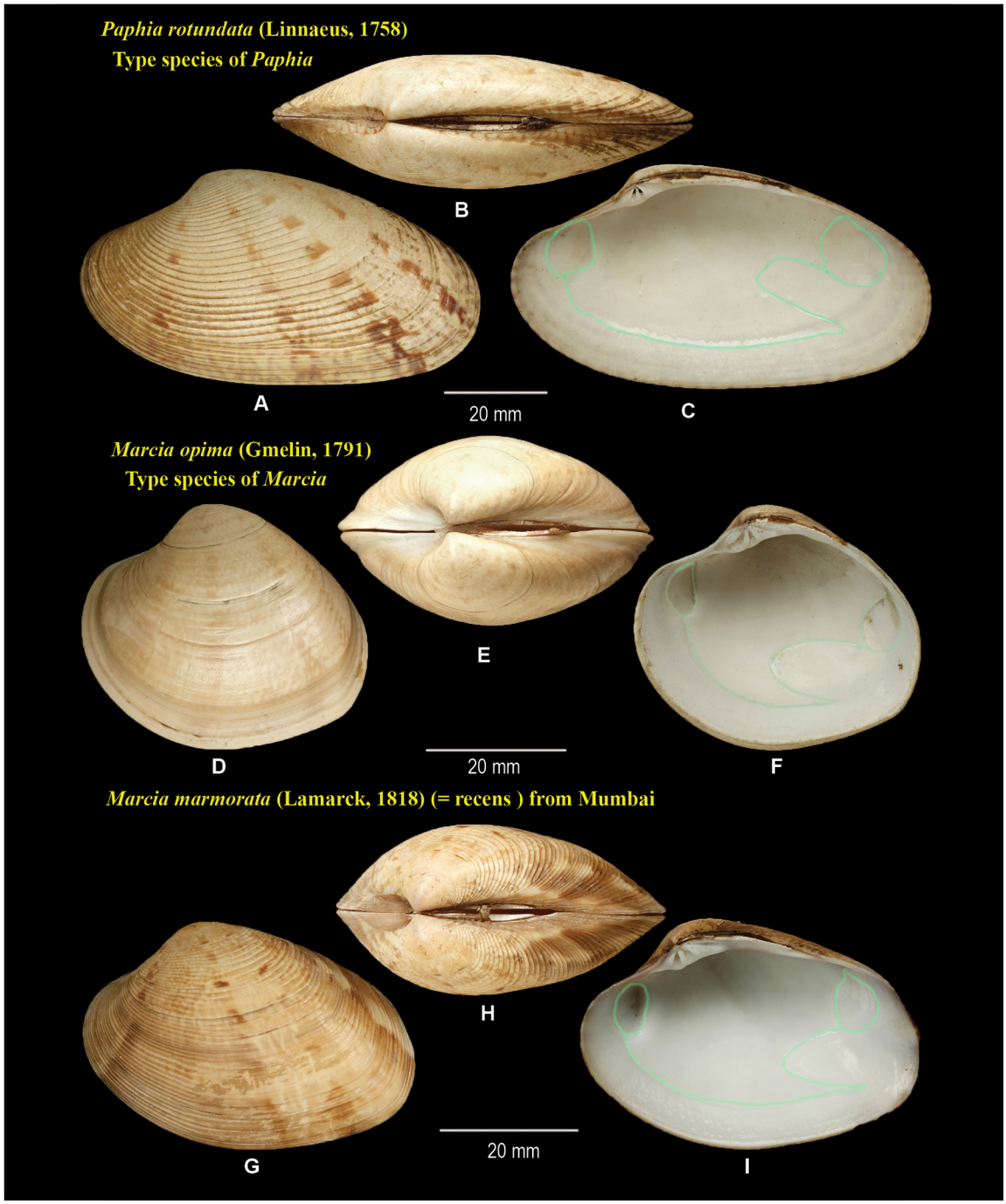

Fig. 2 (A-I). Comparison of the shells of the type species of *Paphia* and *Marcia* and shells of *Marcia marmorata* = *M. recens* from Mumbai. All shells from the Melvill-Tomlin Coll. in the National Museum of Wales, 1955.158.

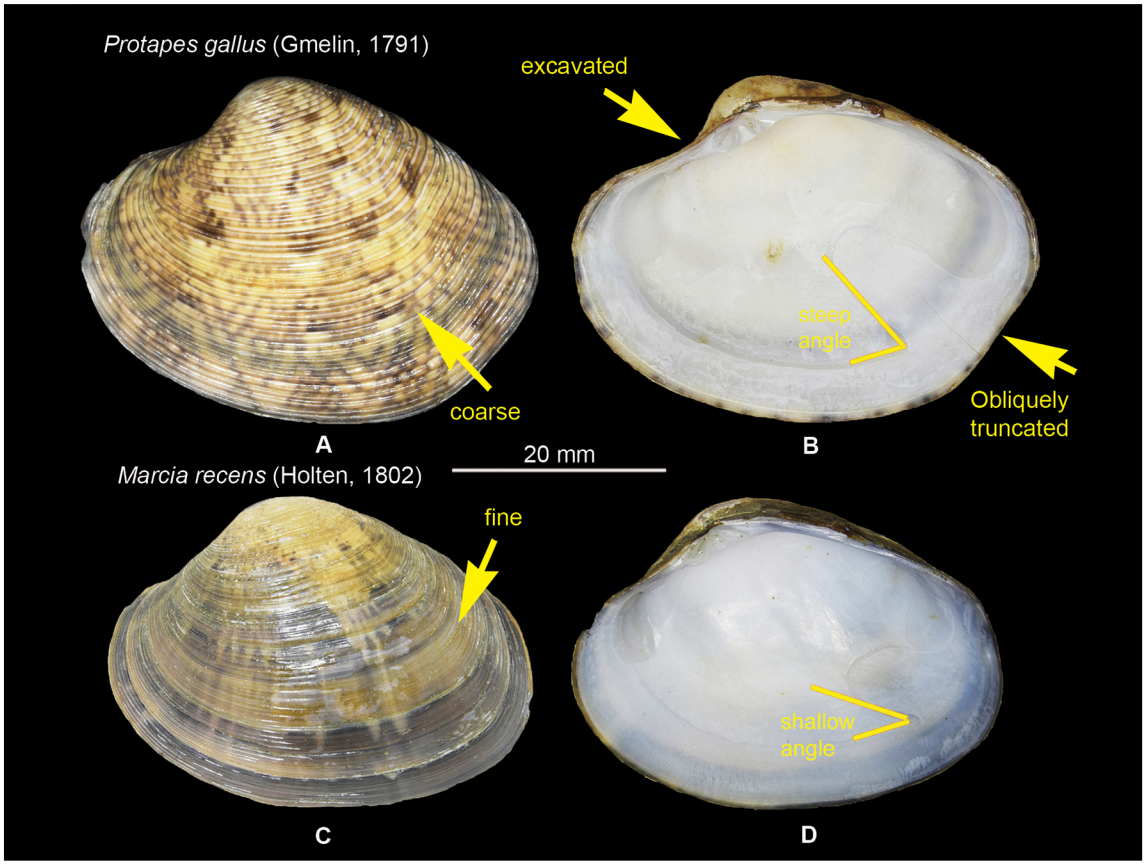

Fig. 3 (A-D). Comparison of the shell of the type species of *Protapes* [*P. gallus* (Gm., 1791)] with that of *Marcia recens* from Ashtamudi Lake.

Table 1. JC69 (Jukes and Cantor, 1969) genetic distances showing the similarity between the topotypic *Marcia recens* and the specimens collected from the southwest coast of India.

	1	2	3	4	5	6	7	8	9
Protapes cf. gallus JQ277809(1)	0								
Protapes gallus MH124117 (2)*	0.02	0							
Protapes ziczac MH124119 (3)*	0.22	0.22	0						
Marcia cf. marmorata HQ703303 (4)	0.28	0.29	0.3	0					
Marcia recens MH124120 (5)*	0.29	0.29	0.29	0.08	0				
Marcia recens MH124121 (6)*	0.29	0.29	0.29	0.08	0	0			
Marcia recens MH124136 (7)#	0.29	0.29	0.3	0.08	0	0	0		
Marcia opima MH124138 (8)*	0.38	0.37	0.33	0.21	0.21	0.21	0.21	0	
Marcia cf. japonica HQ703286 (9)	0.34	0.35	0.36	0.23	0.22	0.22	0.22	0.25	0

*Samples collected from the south west coast of India
#Samples collected from the south east coast of India

this study (*Marcia recens* MH124120 – 31; *Marcia opima* - MH124137 & MH124138; *Protapes gallus* MH124115-17 and *Protapes ziczac* MH124118 & MH124119)

Analysis of sequences generated for this study

The results of the phylogenetic analysis as presented in the phylogenetic tree (Fig. 4) show that the *Marcia* specimens collected from Ashtamudi fall into two clades viz., *Marcia recens* (MH124120 - 31) and *Marcia opima* (MH124137 & MH124138). These sister clades are significantly distinct from the sister clades of *P. gallus* and *P. ziczac* also collected from south Indian waters. The genetic distances of these specimens are presented in Table 1. This confirms that the Ashtamudi short-neck clam is not *Protapes gallus* (=*Paphia malabarica*) as registered by the Marine Stewardship Council. These sequences were generated from properly identified specimens, whose vouchers are available at the Museum collections of the Department of Aquatic Biology & Fisheries, University of Kerala (DABFUK).

The *M. recens* sequences from the type locality Tuticorin (MH124132-36) show genetic similarity with Ashtamudi Lake specimens (Table 1) confirming our morphological assessment that the short-neck clam from the Lake is indeed *Marcia recens*. *Marcia marmorata* considered to be a synonym of *M. recens* from China (Chen *et al*., 2011) falls into a distinct clade from the Indian *M. recens* with a genetic variation of ~8% (Table 1 and Fig. 4). It is therefore likely that the Chinese specimens represent a distinct species (Table 1) of the genus. However the correct identification of Chinese specimens is not possible due to the absence of figures in Chen *et al*. (2011).

The COI sequences of *Protapes gallus* collected from Dharmadam region of Kannur coast showed genetic similarity with the sequences of Chinese *Protapes cf. gallus* (Chen *et al*., 2011) from the NCBI and fell into a single clade in the ML tree (Fig. 4). The *Protapes ziczac* specimen from Kollam coast formed a distinct group in the phylogenetic tree with more than 20% genetic distance from the *Protapes gallus* specimen from the Kerala coast. The results clearly demonstrate the genetic distinction between the species of *Protapes* found on the coast of India. This paper does not intend to explore the wider issues of the systematics of *Protapes* but recognises the need to integrate the Indian data with that of Chinese data presented by Chen *et al*. (2014a,b).

Analysis of sequences generated in this study with that of Sukumaran *et al.* (2019) sequences

Twenty one sequences deposited by Sukumaran *et al.* (2019) used by them for their manuscript were found to be identical (0% genetic distance), further six sequences generated during this study were also identical (0% genetic distance) to the above mentioned Sukumaran *et al.* (2019) sequences. This itself points to their close affinity, however once the phylogenetic tree (Fig. 4) is inspected, it is found that the topotypic *Marcia recens* sequences (MH124132-36) and all the other *M. recens* sequences (Ashtamudi short-neck clam specimens) generated during this study falls into a same clade with the sequences of Sukumaran *et al.* (2019), the branch lengths are also very low indicating very low divergence among the sequences.

The finding of Sukumaran *et al*. (2019) that the Ashtamudi short-neck clam is distinct from *P. gallus* is correct, however their contention that the Ashtamudi clam is *Paphia malabarica* is not true since their sequences are identical and is monophyletic with the topotypic *Marcia recens* sequences. This puts to rest the question about the identity of the Sukumaran *et al*. (2019) sequences and shows that the Ashtamudi clam is indeed *Marcia recens.*

Citing Mikkelsen *et al*. (2006), Sukumaran *et al.* (2019) mention that "*Considerable levels of homoplasy have been detected within Veneridae family when phylogenetic tree was constructed using mitochondrial DNA sequences resulting in overlap at species and genus level...*". Inspecting the Mikkelsen *et al*. (2006) paper we could not find such a statement (that tree built with mitochondrial DNA sequences result in overlap). Mikelsen *et al*. (2006) mention about homoplasy of 'characters' (morphological ones) throughout their paper (this is about the morphological characters), and mention that "*Morphological character mapping on molecular trees retained a high level of homoplasy*", (see abstract of Mikkelsen *et al.*, 2006; page 439) which is not what Sukumaran *et al*. (2019) has reported/paraphrased. Mikkelsen *et al*. (2006) found that the molecular trees yielded better clade

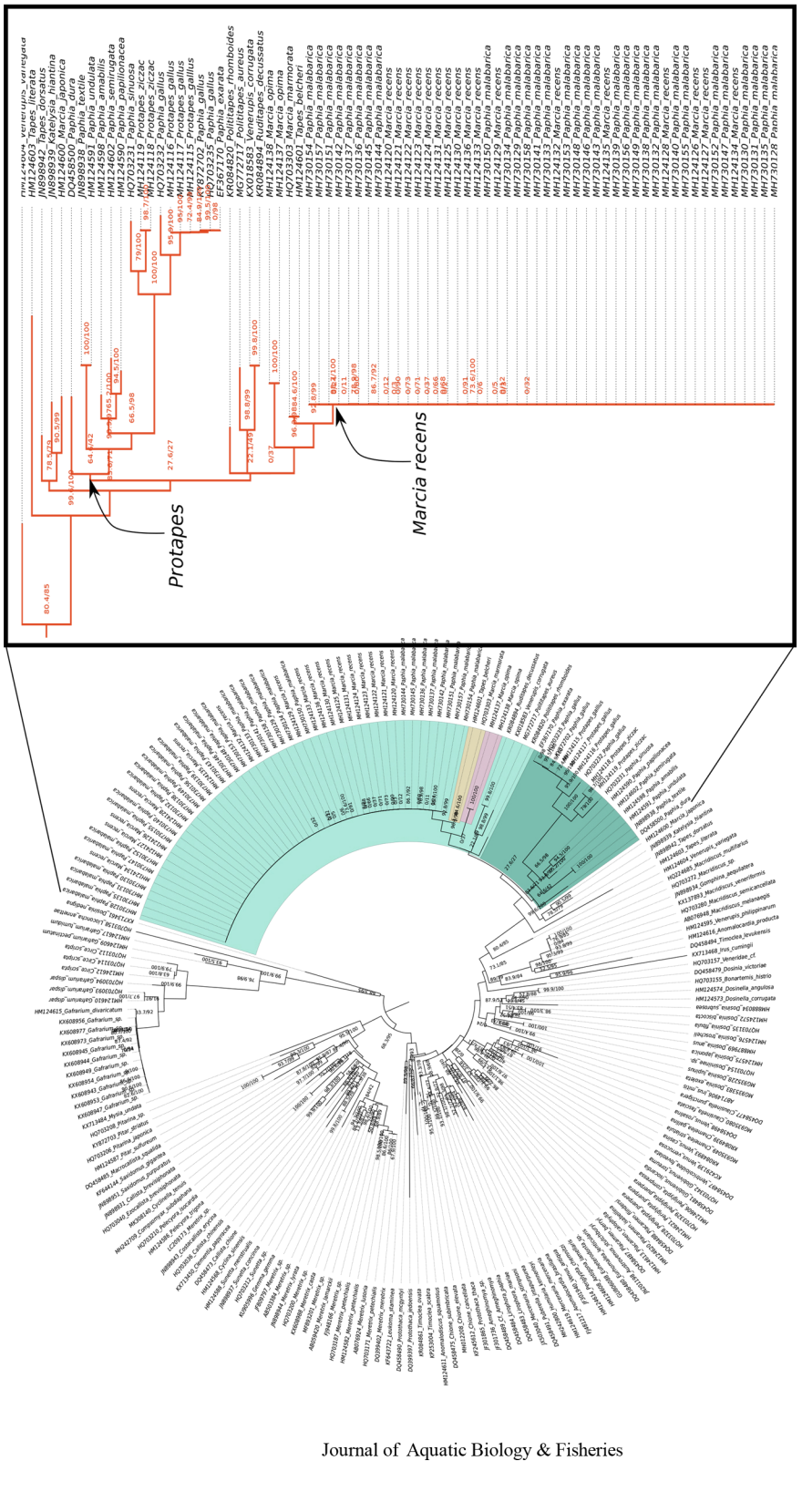

Fig. 4. Phylogenetic tree showing the relationship of the various clam species collected during the present study. The circular tree on the left side has 203 branches and the inset shown on the right side (box) is an enlarged portion highlighting the *Marcia* sequences and *Protapes* sequences.

consistency (see abstract of Mikkelsen *et al.,* 2006; page 439), however they also found that there were considerable amount of incongruency between their morphological character based tree and their molecular tree. Thus they attempted character mapping on a well-supported molecular phylogeny which was also reported in their paper (page 446, page 475 and Figure 12 of Mikkelsen *et al.,* 2006). The authors (Sukumaran *et al.*, 2019) either could not understand the analysis done in Mikkelsen *et al.* (2006) or (understood but) wanted to mis-cite that paper to support their false claim.

Does the correct taxonomy matter?

Consistency in zoological nomenclature has developed in order to give a regulated and internationally accepted naming system based primarily on the principle of priority. Deviation from these principles can be proposed and arguments made to the Commission for Zoological nomenclature. Any attempt to retain the name *Paphia malabarica* is unnecessary and would involve the numerous steps involving both the generic and species names. We believe that the conservation of invalid names is not warranted when the issue has been one of misidentification and when a valid and widely accepted alternative is available.

Sukumaran *et al*. (2019) precisely state that the correct taxonomy is important for commercial species as did Arathi *et al*. (2018). The latter cited the need to have consistency in order to allow comparability between culture methods, biochemical and physiological data. We believe that trying to retain the name *Paphia malabarica,* and using it in literature without considering the results of morphological analysis (Arathi *et al.*, 2018) and molecular analysis in this paper, is confusing as this name does not conform to the wider understanding of venerid systematics. This practice could lead to inappropriate comparisons across studies. The results provided in this paper thus helps in clarifying the taxonomic status of the Ashtamudi short-neck clam. We show that the dominant clam species in Ashtamudi is *Marcia recens* and that the usage of the name *P. malabarica* is wrong and has to be avoided.

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