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Evolutionary systematics of freshwater snail *Melanoides tuberculata* (Cerithiodea: Thiaridae) from South East Asia-a brief review

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Abstract
Evolutionary systematics is the phylogenetic systematic study of the diversity of organisms, considering taxonomy, morphological disparity, genetic variability, and the investigation of causative factors responsible for such variations. The species inventories of the family Thiaridae occurred in the past are centered on morphology, anatomy and phylogenetic relationships within and among the taxa. The freshwater thiarid, *M. tuberculata* with species specific polymorphisms and pantropical distribution is the best models to understand the mode of speciation and evolution. However, the evolutionary systematics of the *Melanoides* in Southeast Asia is poorly understood and details of the taxonomy and phylogeny still remain unresolved. This review presents the existing information on evolutionary systematics of *M. tuberculata*. Resolving evolutionary systematics using the molecular genomic methods are emphasised.

Keywords: Phylogenetics, brood pouch, speciation, morphs, biogeography

Introduction

With their polymorphic features and informative soft body parts the freshwater cerithioideans are highly suitable for providing some fundamental insights into the mechanisms of the genesis of biodiversity, its pattern in historical biogeography, and the underlying processes of speciation and radiations (Glaubrecht, 2009) [8, 10]. Freshwater Thiarids belonging to this taxon are ecologically important and well represented in tropical regions of Southeast Asia, with numerous genera and species (Glaubrecht, 2011) [9]. They have adapted to wide array of ecological conditions, have proven to be highly suitable models to study systematic, ecological, paleontological, evolutionary and zoogeographic phenomenon. Their ability to exploit a range of reproductive strategies (gonochorism to widespread parthenogenesis; oviparity to viviparity) has enabled them to colonize new areas quickly, with some even reaching 'pest species' status (Healy and Wells, 1998) [14].

Melanoides tuberculata is renowned as one of two globally invasive thiarid gastropods occurring in a wide variety of perennial or temporary, freshwater or brackish habitats (Raw *et al*., 2016) [23]. The native range of *M. tuberculata* extends through East Africa, across the Middle East and to Southeast Asia (Facon *et al*., 2003) [4]. Their effectiveness as colonizers is heightened by their tolerance of low oxygen conditions and disturbed habitats, their rapid growth, high fecundity and ability to maintain high population densities. This species in particular has an elongated, highly turreted spire on their shells; they display a large phenotypic plasticity, which is due to individual, ecological and or geographical factors often dovetailing and intertwined (Glaubrecht and Podlacha, 2010) [10]. Within its native and new range, it is possible to find genetically and phenotypically distinct morphs (Samadi *et al*., 1999) [24], which may have either African or Asian evolutionary origins due to human-mediated spread (Facon *et al*., 2003) [4]. These different morphs display different life-history traits and vary genetically within the clones as well as between the clones. Anatomically this species can be recognised by the presence of a brood pouch located in the head-foot, associated with various viviparous modes, including intra-marsupial nourishment and giving birth to crawling juveniles with shells comprising several whorls that develop before hatching (Glaubrecht, 2006; Glaubrecht *et al*., 2009) [12, 8, 10].

These species exhibit viviparous matrotrophy by the presence of pseudoplacenta in the brood pouch (Glaubrecht, 2006) [12]. The anatomical variations in reproductive systems are misunderstood, because of concurrent and convergent evolution of the Thiaridae, from ancestors common to the marine families. This review aims to know the phylogeny, morphological similarities, brood pouch analysis, biogeographical distribution South East Asian *Melanoides* to unravel evolutionary relationships. Thus, the framework of this review is to resolve the evolutionary systematics of *Mealnoides tuberculata* through morphometrics, reproductive anatomy, phylogenetics and phylogeography.

Although South East Asia is speciose in terms of freshwater molluscs, studies have been confined to species checklists with limited taxonomy. Important taxonomic contributions on freshwater molluscs of South East Asia including India are of Benson (1836) [1], Blanford and Godwin Austen (1908) [2], Ramakrishna and Dey (2007) [22]. But there has been no study on South East Asian *M. tuberculata* morphs to reveal its systematic position, phylogenetic relationships and evolutionary relationships.

Glaubrecht (2004) [7] proposed that the thiarids status can be assessed using the morphological and anatomical differences combined only with recent advances in molecular methods. i.e. by comparison of genetic distances. Samadi *et al*., (1999) [24] studied the population structure of *Melanoides tuberculata* from the Middle East to Africa using morphological variability and microsatellite analysis. Pointier *et al*. (1993) [21] showed that the morphs display different life history traits, that may play a significant role in the competition between morphs. *M. tuberculata* some rare events of sexual reproduction are reported (Samadi *et al*., 1999) [24]. Some bisexual populations have been detected in Israel (Heller and Farstay 1990) and in Martinique (Samadi *et al*., 1997). The ratios of shell-diameter/shell-height and penultimate-whorl diameter/shell-diameter differ significantly between males and females due to the absence of the brood pouch in males (Heller and Farstay 1989) [5]. Investigations on sperm ultrastructure of *M. tuberculata* have been carried out (Hodgson and Heller 1990) [16] but are incomplete in terms of mature sperm features. Later, Healy and Glaubrecht (2018) [13] found a close relationship between *T. amurula* and *M. tuberculata* and other Cerithiodean families exhibiting four equals sized eusperm mitochondria. Dechruksa *et al*., (2013) [3] evaluated the identity of "*Melania" jugicostis* and found it as distinct species differing in all the characters in comparison with *Melanoides tuberculata*. Although, thiarids were used as reference materials in most of the studies, the new mode of reproduction *i.e.* parthenogenesis was underestimated due to the variability in reproductive structures (Glaubrecht, 1996) [11].Unambiguous evidence of sexual reproduction has been reported in Martinique (Samadi *et al*. 1999) [24], and concerns two morphs detected in the 1990s. Morphological and micro satellite data showed that these two morphs are hybrids between pre-existing invasive morphs in Martinique (Samadi *et al*., 1999) [24]. These hybridization events involved unreduced female gametes from one morph and reduced (meiotic products) male gametes from the other one, inducing an increase of the ploidy level of the hybrids. Australian freshwater thiarids showed euviviparous reproductive stratergies, interspecific and interspecific variations in reproductive structures, quantitative differences between the species which is expected to remain true with respective data from other eu-viviparous thiarids from other parts of the world (Maaß and Glaubrecht, 2012). Glaubrecht (1999) [6] noted that viviparity although important for speciation in some cases, the ultimate cause for their radiation in freshwater in general. He also stated that, as the species is rapid colonizer in aquaria and hot springs, their distribution pattern is human mediated in addition to the autochthonous range in certain parts of the world (Glaubrecht 2000, 2009) [8, 10]. Pointier (1992) [20] studied the invasion of morphs of *M. tuberculata* in Martinique and investigated their life history traits. It is evident that k-strategist species would be efficient invading species, aided by parthenogenesis and viviparity. It is also not known that whether the invasions to the non-native regions is due to vicariaence or dispersal, splitting of the continents leading to pantropical distribution, remains to be tested. Ostrovsky *et al*., (2016) [19] showed that the provisioning of developing young is associated with almost all known types of incubation chambers, with matrotrophic viviparity more widespread (20 phyla) than brooding (10 phyla). Glaubrecht *et al*., (2009) [8, 10] described that those species with eu-viviparous mode show "kbp"-strategists, i.e. possessing less juveniles in their brood pouch and, thus, a lower intrinsic rate of reproduction, wherein maternal investment during reproduction is higher. They evolve under density independent conditions compared to K-selected species that have low reproductive rates evolving under density dependent. They found that kbp-species such as *M. tuberculata* have a less restricted, often widespread distribution on the Australian continent. The survival of k-statergic species could be correlated to the seasonality and rainfall data to find the influence of ecological conditions in their geographical localities. It seems that K-strategist coenogastropods (compared with r-strategist pulmonates) would be efficient invading species, aided by parthenogenesis and viviparity which requires further investigations (Glaubrecht *et al*., 2009) [8, 9].

The molecular phylogeny has brought about transformation that may change the classification of many phyla (Glaubrecht 2009) [8, 10]. Evolutionary systematics of freshwater thiarids of Southeast Asia is poorly understood and information about the biogeography and phylogeny are lacking (Glaubrecht *et al*., 2009) [8, 10]. However evolutionary systematics approach has been applied to genus *Sermyla* of family Thiaridae but not for genus *Melanoides* (Lentge-Maab *et al*.,2021) [17]. Samadi *et al* (1999) [24] have described 16 different morphs of *M. tuberculata* worldwide, each apparently corresponding to a single clone. Within populations from both the original and invaded areas, several morphologically distinct morphs often coexist but the amount of genetic divergence among morphs is unknown. The knowledge on the similarities and differences in reproductive characters and analysis of brood pouch of the morphs would help in tracing their zoogeography. The adaptability of reproductive structures and ecological factors can be correlated that would help in reconstructing the evolutionary ecology of these freshwater thiarids in general and *M. tuberculata* in particular. Hence, combination of phylogenetic techniques, reproductive anatomy and morphometrics are required to solve these Darwinian mysteries.

Conclusion

The thiarid, *Melanoides tuberculata* is a global invader, and cause speciation in the regions of colonization. However, the recent studies detailing the evolutionary systematics of this species are lacking. Comparison of different morphs based on brood pouch anatomy and developmental stages of embryos would help to understand modes of viviparity and the intraspecific variations of brood pouch contents of the individual morphs. The use of cutting edge molecular genomic methods along with morphometric and reproductive analysis is expected to resolve the phylogeny of the *Melanoides* morphs. In addition, obtaining historical data to reconstruct the biogeography, is another essential prerequisite for the systematic revision of these species.

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