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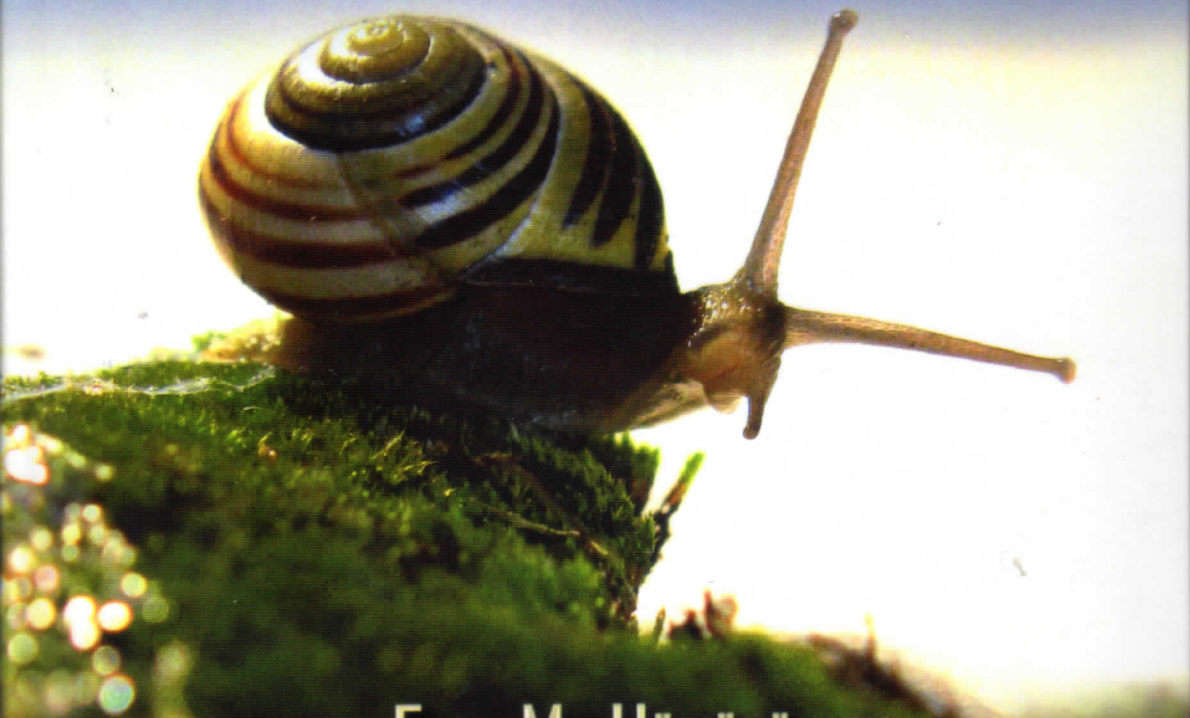
BIOLOGY, ECOLOGY AND CONSERVATION



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Snails

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Emil M. Hämäläinen
and
Sofia Järvinen
Editors

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Chapter 3

MELANOIDES TUBERCULATA: THE HISTORY OF AN INVADER

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ABSTRACT

The thiarid snail *Melanoides tuberculata* (Müller, 1774) has demonstrated an impressive capacity to invade a range of tropical and subtropical aquatic ecosystems. This species exhibits characteristics often mentioned to increase invasion ability.

It is an ovoviviparous species with parthenogenetic reproduction and it has life history traits characteristic of 'r' strategists (early maturity,

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relative short life span, iteroparity and high fecundity). This is a euryoic species, but temperature may be an important determinant of its distribution. *Melanoides tuberculata* has been reported in literature as a nuisance species in some tropical fish aquaria and in rice paddies, and invading the heat exchanger of an electric power-plant, causing complete clogging of the filters.

Molecular studies suggest an Asian origin for numerous morphs of this species, followed by introduction to both Africa and America (from northern Argentina to southeast USA). The New World was invaded several times by several morphs of *M. tuberculata* from a large number of Old World sources. These morphs currently coexist and new morphs were created in situ by hybridization (as a consequence of rare events of sexual reproduction), and there is evidence of competitive replacement between them.

In some places, no impact associated with this species on the native molluscan fauna has been observed, but in Brazil and Argentina, preliminary data indicate that native populations of the Thiaridae were replaced by populations of *M. tuberculata.*

Although *M. tuberculata* is used as a control of schistosomiasis (by competitive replacement of the planorbid *Biomphalaria glabrata*), it also plays an important role, as an intermediate host, in the epidemiology of several trematode species which can be harmful to a number of vertebrate species, including man.

Despite the importance of this species (it can cause ecological risks, health and economic), much remains yet to be known and done to prevent its spreading. The summarized information of *M. tuberculata* in this chapter is expected be useful to shed light on this species, propose new hypotheses, and to design plans to control the invasion and its consequences.

INTRODUCTION

The freshwater gastropods are a diverse group that comprises in continental waters ca. 4,000 valid described species, exhibiting a wide range of life history traits, reproductive modes, and ecological requirements.

Among freshwater snails, some have gained special attention as "invasive species". This is due to economic, ecologic and/or sanitary consequences where the pulmonates (Physidae, Lymnaeidae, Planorbidae) and parthenogenetic species, such as *Melanoides tuberculata* (Müller, 1774) are listed among the most successful colonizers (Strong et al., 2008).

In particular, *M. tuberculata* constitutes a good example of how the combination of life history traits, genetic background and human facilitated

dispersal can contribute to the introduction and establishment of new populations of the species in a novel environment.

Which Characteristics of *Melanoides tuberculata* Make it a Good Invader?

Invasive species (species that establish self-sustaining populations outside of their native range) are said to exhibit some characteristics, often mentioned to increase invasion ability (Lodge, 1993). These include: r-selected traits, high dispersal rate, single parent-reproduction, high genetic variability, phenotypic plasticity, large native range, eurytopy and polyphagy. *Melanoides tuberculata* exhibits most of these characteristics.

Morphologic and Genetic Characteristics

Melanoides tuberculata is an operculated snail presenting extensive phenotypic variation in terms of shell shape, sculptures and pigmentation, and allows for the definition of discrete entities referred to as morphs (Pointier, 1989; Escobar et al., 2009). This morphological variation is inheritable and more than 27 morphs are actually known (Pointier et al., 1992; Facon et al., 2003). Currently, some of these morphs co-exist, and new morphs were reported to be created by hybridization with competitive replacement between them (Facon et al., 2005). Each morph usually corresponds to a single genetic clone or parthenogenetic line, with few exceptions, and morphs are separated by considerable genetic distances (Samadi et al., 1998, 1999, 2000). However, clonal diversity in *M. tuberculata* seems to not be the product of an adaptation to a particular ecological niche, as the clones are generalist and the species is considered to fit the "General Purpose Genotype" (Lynch, 1984), in which the same clone can successfully colonize a variety of habitats. Such is the case of two clones co-occurring in all the freshwater habitats of the French Polynesian Islands (Myers et al., 2000; Vrijenhoek and Parker Jr., 2009).

Additionally, sexual dimorphism and phenotypic plasticity (often referred to as ecophenotypic variation when the precise environmental variables involved are unknown) are proposed as sources influencing the morphology. The former, detected as a marked within-morph variation between males and females in populations when males exist, and the latter as an extensive spatial and temporal variation within clones, representing alterations to the phenotypic expression of particular genotype due to an environmental variation (Samadi et al., 2000).

Diet Composition

The diet of this snail consists mainly of benthic, epiphytic and periphytic algae; bacteria, organic particles deposited on the sediment; and decaying plants (Dudgeon, 1989; Pointier et al., 1991; Ben-Ami and Heller, 2005). Gut analyses indicate that *M. tuberculata* indiscriminately consume microalgae (e.g. diatoms) and fine detritus from solid surfaces (Subda Rao and Mitra, 1982). Furthermore, the species was observed to be able to benefit from feeding on dead animal tissue (Rader et al., 2003). Thus, it appears that *M. tuberculata* is a generalist herbivore and detritivore that will feed on a variety of plant and animal tissue.

Habitat Requirements

This snail inhabits a wide range of aquatic environments, either lentic or lotic, at depths ranging between 0.25 and 3.7 m (Murray, 1975; Suriani, 2006; Vasconcelos et al., 2009; Peso et al., 2011). It was found to be associated with various types of substrates (rock, gravel, mud, clay and sand, Figure 1), and it is often associated with macrophytes and substrates introduced by man (e.g. plastic, wood) (Da Silva et al., 1994). Its presence has been detected in rivers and streams of different flow rates, lakes, reservoirs, dams, and levees. The ability of *M. tuberculata* to resist displacement by rapid currents is greater than South American native thiarids (*Aylacostoma spp.*) (Quintana et al., 2001-2002).

Nonetheless, this snail was vastly diminished or was absent in steep rivers with fast current velocities (Pointier et al., 1994), and it can reach high densities in ponds and gently flowing waters (Pointier et al., 1993). Although *M. tuberculata* is abundant in some swiftly flowing canals (42-51 cm s^{-1}), it primarily occurs in macrophyte beds where current velocities are reduced; being also abundant in springheads, marshes, and flowing channels with current velocities lower than 15 cm s^{-1} (Dundee and Paine, 1977; Rader et al., 2003). Moreover, it is able to colonize recent water bodies on a permanent basis in a short period of time (Facon et al., 2004).

Melanoides tuberculata is able to exploit environments with different degrees of eutrophication (from oligotrophic to hypereutrophic). Moreover, it is tolerant to low levels of dissolved oxygen (Neck, 1985) and is also highly resistant against pollution, such as what one might expect in an urban environment (Dudgeon, 1989). It has a great resistance to desiccation, making it able to colonize temporary aquatic environments (Dudgeon, 1986). In this regard, Pointier et al. (1992) argue that this snail is absent or rare in periodically dry environments.

Figure 1. Shells of *M. tuberculata* on sand.

However, other studies found that *M. tuberculata* is resistant to a lack of water for prolonged periods of drought (i.e. 26 months), and showed that the survival rate of an individual will decrease with an increase in drying time (Abílio, 2002).

Melanoides tuberculata can colonize environments within a wide range of salinity and height. Live specimens have been captured in waters from freshwater environments at 1,500 m altitude, up to estuarine waters with salinity levels as high as 33 ppt -parts per thousand- (Russo, 1973; Berry and Kadri, 1974; Roessler et al., 1977; Starmühlner, 1979; Dudgeon, 1986, Wingard et al., 2008).

However, recent temperature tolerance studies which predict the species' potential distribution (Mitchell and Brandt, 2005), as well as previous data (e.g. Murray, 1971; Neck, 1985), indicate that temperature may be an important determinant of its distribution, suggesting that waters with temperatures <18ºC, or greater than 32ºC, will probably not support *M. tuberculata*.

It has been registered with greatest abundance between 21ºC and 30ºC (Ismail and Arif, 1993; Laamrani et al., 1997; Duggan, 2002), and has been found hibernating in the wild during the colder months (Livshits and Fishelson, 1983). Nonetheless, after one year at constant temperatures in an aquarium (25ºC), these snails had lost their hibernating habits (Livshits and

Fishelson, 1983). In areas where daytime water temperatures can exceed 35°C, *M. tuberculata* is primarily crepuscular, or nocturnal spending most of the daylight hours buried in mud or sand (e.g. Subda Rao and Mitra, 1982; Pointier, 1993).

In captivity, *M. tuberculata* showed nocturnal habits, with most of the individuals staying huddled in a corner of the aquarium or buried in the sand during the day, increasing its activity by decreasing light intensity (Livshits and Fishelson, 1983). Additionally, a study assessing the effects of predation risk (via chemical cues) and conspecific density on temperature selection of *M. tuberculata*, showed that this species seems to modify its thermoregulatory behavior when exposed to chemical cues (i.e. predation risk). The study also suggests that snails favor predator avoidance over thermal selection when presented with both demands (Gerald and Spezzano Jr., 2005).

Life History and Reproductive Characteristics

This prosobranch snail is an ovoviviparous, gonochoric species with polyploidy races (Ben-Ami and Heller, 2008; Escobar et al., 2009). Its reproductive system is extremely simple in structure and histology, lacking all the glandular developments common in most mesogastropods (Berry and Kadri, 1974). Their eggs, which are small (50 X 70 μm), pass into a cephalic brood-pouch where they develop to juveniles before emergence, with up to 6 shell whorls. The number of developing young in the brood-pouches varies from 1 to 91 (Berry and Kadri, 1974; Subda Rao and Mitra, 1982; Livshits and Fishelson, 1983; Pointier et al., 1993), different from *Aylacostoma* species that have an average of only 3 to 5 (Quintana et al., 2001-2002). However, other authors found even higher numbers of embryos, counting more than 450, noting that juveniles can remain within the adventitious pouch for long periods of time as a result of inhibition of their release during adverse season (Dudgeon, 1986; Bedê, 1992). Moreover, although the survivorship of newly born snails has not been measured, brooding their young and releasing them at a larger size may be due to a strategy designed to enhance their survivorship (Stearns, 1977).

Juveniles commonly emerge from the brood-pouch most between nightfall and midnight, and normal emergence seems to require a diurnal alternation of light and dark. In continuous darkness, brood-pouch counts increased markedly, perhaps as a result of greater activity and feeding during darkness (Berry and Kadri, 1974). Thus, the number and size of juveniles in the brood-pouches varies in different environments, and generally increases with the shell height of the parents, implying variation in fecundity (Berry and Kadri, 1974; Livshits and Fishelson, 1983). Newly born *M. tuberculata* measure between 1.5 to 2.0 mm in length, grow at a rate of about 2.5 mm per month and can begin reproduction with an initial shell height of 8.3 mm after 90 days of life (Berry and Kadri, 1974; Livshits and Fishelson, 1983; Dudgeon, 1986; Pointier et al., 1993; Quintana et al., 2001-2002). However, Ben-Ami and Hodgson (2005) found embryos in snails as small as 7 mm in length. Snails greater than 25 mm stop producing gametes, but can continue to grow (Livshits and Fishelson, 1983). Average adults of *M. tuberculata* may grow up to 80 mm (Murray, 1975), but they generally vary in size between 20 to 40 mm (Berry and Kadri, 1974; Dudgeon, 1982; Livshits and Fishelson, 1983; Neck, 1985; Pointier, 1989).

This species has an average lifespan of 2-3.5 years (Freitas et al., 1987; Bedê, 1992). It presents with high birth and low mortality rates, so it can double its number of individuals in two weeks (Abílio, 2002). Also, it is able to maintain high population densities for a long time; that is, intraspecific competition does not seem especially severe (Pointier et al., 1991). In fact, there are frequent reports of population density between 2,000 to 15,000 individuals m^2 (Freitas et al., 1987; Lévêque, 1972; Pointier and McCullough, 1989; Thomas and Tait, 1984), reaching over 50,000 individuals m^2 in some cases (Murray and Wopschall, 1965; Roessler et al., 1977).

An important issue to consider is that most populations reproduce primarily through apomitic parthenogenesis (Jacob, 1957, 1958; Berry and Kadri, 1974). Additionally, some populations consist of only females, with the existence of but a few sterile males (Dudgeon, 1986). However, evidence of sexual reproduction has been found in populations where male frequencies reached up to 66% (Livshits and Fishelson, 1983; Heller and Farstey, 1990; Samadi, 1998, 1999; Ben-Ami and Heller, 2005). Sexual reproduction was suggested by Heller and Farstey (1990), based on the evidence of a higher frequency of fertile males combined with the higher genetic diversity of bisexual populations (Ben-Ami and Heller, 2005, 2007).

DISTRIBUTION AND INVASION

Native Distribution

There is still some considerable uncertainty regarding the native distribution of *M. tuberculata*. The species was described from the Coromandel Coast of India in 1774 and its distribution, in publications in the early 20th century, includes the intertropical belt of the Old World from Africa to Southeast Asia (Pilsbry and Bequaert, 1927; Facon et al., 2003; Escobar et al., 2009). *Melanoides tuberculata* is characteristic of South Asia, Indochina, the Philippines and South Pacific islands, India, Arabia, much of Africa, Madagascar and northern Australia. Furthermore, it is also found in European Mediterranean countries and in environments consisting of the hot springs in Austria, Germany, Czech Republic, Slovakia, and Hungary (Quintana et al., 2001-2002; Rader et al., 2003).

Non Native Area: An Example from the New World

The existence of populations of *M. tuberculata* on the American Continent has been known since the mid-20th century (Quintana et al., 2001-2002), and involves a striking anthropogenic dissemination process. This is thanks to multiple introductions, mainly as the result of the trade of aquarium plants (Madsen and Frandsen, 1989), not excluding the possible introduction through animal vectors such as birds, fish and mammals (Maguire, 1963; Correa et al., 1970; Amaya-Huerta and Almeyda-Artigas, 1994; Escobar et al., 2009).

The first record of the species on the American Continent comes from North America, where it was probably introduced by the aquarium industry in the 1930's (Murray, 1971). By the mid-1960's *M. tuberculata* was reported from Texas, Arizona (USA), followed by a rapid expansion in nearly all American countries (Rader et al., 2003; Wingard et al., 2008). However, introduction from the Old World to the American Continent was not a unique and isolated event. Recent genetic studies demonstrated than at least six independent founding events occurred, in which the central area of the New World was invaded by African lineages; and the south of the American Continent; as well as part of Africa, by Asian lineages (Facon et al., 2003; Vogler et al., 2008).

Today, the species is established or reported in almost all of the regions between north Argentina and Florida, USA (Peso et al., 2011), including the West Indies, as well as Venezuela, Colombia, Peru, Brazil, and Paraguay (Escobar et al., 2009; Peso et al., 2011).

In the most of the invaded countries, the origin of their introductions remains unknown. However, according to the country in which the species was recorded, different suggestions about its origin of introduction have been made. For example, the origin in Brazil is suggested to probably be linked to the plant and freshwater ornamental fish trade, given the first record of *M. tuberculata* in the state of São Paulo was in aquarium hobbyist stores in the city of Santos (Fernandez et al., 2003). In contrast, in Argentina and Paraguay, the origin of introduction is suggested to be linked to passive distribution down the Paraná River (as it flows from Brazil), perhaps on floating vegetation such as macrophytes, which provide a vehicle for rapid downstream dispersal (Peso et al., 2011). Nevertheless, in Argentina, the introduction via the commercial trade was also recently reported, due to the species has become widely available in pet shops and is being sold on the Internet (Gutiérrez Gregoric and Vogler, 2010).

Existing and Potential Impact in Non-Native Areas

Impacts on Native Fauna

The ability of *M. tuberculata* to reach high densities, combined with a large body size, suggests that competition between this species and other snails might be severe; to the advantage of *M. tuberculata* (De Freitas and Dos Santos, 1995). Several studies in the New World, where the species have become abundant, recorded a significant density decline of some native gastropods. In Rio de Janeiro, indigenous *Pomacea lineata* (Spix, 1827) (Ampullariidae) and *Biomphalaria glabrata* (Say, 1818) appear to be affected by *M. tuberculata* (Fernandez et al., 2001). Also in Brazil, abundant populations of *Aylacostoma tenuilabris* (Reeve, 1860) (Thiaridae) on the Tocantins River, have been replaced by dense populations of *M. tuberculata* (Fernandez et al., 2003). In Argentina and Paraguay, replacements of other thiarids species was predicted after *M. tuberculata* was reported for the first time (Quintana et al., 2001–2002), but no experimental study has been performed. However, it is possible that native communities in the invaded aquatic systems may actually be impacted (Peso et al., 2011). Roessler et al. (1977) found that the growth and reproduction of a Florida snail, *Neritinia virginea* (Linnaeus, 1758), declined in the presence of *M. tuberculata,* presumably because of resource competition (Rader et al., 2003). Also, several reports have documented the reduction, and even disappearance, of populations of the planorbid snails, *Biomophalaria glabrata* and *B. straminea* (Dunker, 1848), parallel with the establishment of *M. tuberculata* in Brazil and the Caribbean (Pointier and McCullough, 1989; Pointier et al., 1994;

Guimarães et al., 2001; Derraik, 2008). Interestingly, *M. tuberculata* has been intentionally introduced as a biological control to eliminate *B. glabrata* because it transmits the deadliest of all human trematode parasites, the blood fluke *Schistosoma mansoni* (Rader et al., 2003). However, biological control using *M. tuberculata* must be considered with caution because of the medical significance of this species (Pointier, 1999) (see below).

Additionally, other invertebrates which scrape algae from solid surfaces and consume decaying vegetation may also be at risk because of direct competition from *M. tuberculata*. Also, grazers, detritivores, and predators that depend on them could be altered and harmfully impacted by the species (Rader et al., 2003).

Impact on Animal and Human Health

Melanoides tuberculata, like many other gastropods of inland waters, has been reported as an intermediate host and transmission vector for trematode parasites that are dangerous to humans, livestock, and wild animals (Rader et al., 2003). A recent list of flukes species transmitted by the snail includes 17 families, 25 genera and 37 species, including 11 trematodes reported as adults from man (Pinto and De Melo, 2011). Given the pantropical distribution of the species, *M. tuberculata* constitutes one of the most important intermediate hosts in the world for numerous human and vertebrates flukes, including: *Clonorchis sinensis, Centrocestus formosanus, Paragonimus westermani, Paragonimus kellicotti, Angiostrongylus cantonensis, Loxogenoides bicolor, Transversotrema laruei, Stictodora tridactyl, Gastrodiscus aegyptiacus, Philophthalmus gralli, P. distomatosa, Haplorchis pumilio, Haplorchis sp.*, and several species of Heterophydae (Quintana et al., 2001-2002; Thiengo et al., 2001; Bogéa et al., 2005; Derraik, 2008).

Among the species that affect humans, *Clonorchis sinensis* is a trematode responsible for serious bile duct and pancreas diseases of both man and domestic animals, whose second intermediate hosts are about 80 freshwater fish species. Human infection occurs by consuming raw fish infected by this parasite (Souza and Lima, 1990). However, the likelihood of infection may be significantly compounded by utensil contamination with metacercariae, which may be an important route for *Clonorchis* infection in humans (Derraik, 2008).

Centrocestus formosanus is responsible for a food-borne intestinal infection in humans, with cases reported in Asia, Mexico and Colombia (Pointier, 1999; Scholz and Salgado-Maldonado, 2000; Velasquez et al., 2006). The reservoirs of the parasite include rats, cats, dogs, chickens and ducks; raw freshwater fish are the main sources of human infection (Yu and Mott, 1994; Pointier, 1999). As with other trematodes, human infection occurs via the consumption of raw or improperly cooked fish, although the use of contaminated kitchen utensils may also be a significant route for human infection (Derraik, 2008).

Paragonimus westermani is a trematode which is housed in the lung cavity of man, whose second intermediate hosts are freshwater crabs and certain species of shrimp. On the American Continent, human paragonimiasis caused by other *Paragonimus* species (considered zoonotic in this case, as in their cycle would contribute native gastropods) is endemic in Peru and Ecuador (Quintana et al., 2001-2002). Cases have also been reported in Mexico, Honduras, Costa Rica, Colombia and Brazil. As in the case of *Clonorchis sinensis*, infection is acquired by eating raw meat, in this case of crabs.

Melanoides tuberculata is also an intermediate host of the rat lung-worm *Angiostrongylus cantonensis*, a parasite that causes eosinophilic meningitis in humans. This is usually a self-limiting disease, which may occasionally lead to serious complications and consequent death (Derraik, 2008). This parasite has been detected in several continents and is transmitted by several mollusk species, both terrestrial and aquatic (Pointier, 1999, Maldonado Jr. et al., 2010). Human infection is caused by the ingestion of infected snails (more common in terrestrial mollusks).

However, according to Derraik (2008), it is possible that food plants, such as watercress, cultivated in unhygienic locations where infected snails are present, may also lead to human infection.

In addition, it has been suggested that human infection is also acquired by ingesting water contaminated with mucus which contains *A. cantonensis* larvae secreted by the mollusk. Furthermore, it seems that infection with *A. cantonensis* can occur in children who have been playing with host snails (Derraik, 2008).

Other Impacts

Although numerous cases of *M. tuberculata* becoming a nuisance species in tropical fish aquaria have been reported (De Kock and Wolmarans, 2009), almost no studies have attempted to demonstrate any economic negative effects on the American Continent. However, the species has become plentiful in rice paddies in a province of South Africa, and was also recorded as invading the heat exchanger of an electric power-plant, clogging the filters and resulting in a malfunctioning of the entire system (De Kock and Wolmarans, 2009).

Conclusion

Melanoides tuberculata has the potential to be invasive on account of some of its ecological and biological characteristics: it has great adaptability and the ability to tolerate extreme environmental conditions. Its reproductive biology, and mainly its ability to reproduce by parthenogenesis, also constitutes the prerequisites associated with the invasive potential of the species. The evolution of parthenogenesis in freshwater mollusks acts as "Reproductive Assurance", facilitating colonization by increasing the likelihood of reproduction in a small number of colonists (Dillon, 2000; Heath, 1977). The wide spread and prevalence of *M. tuberculata,* in terms of biomass in a variety of tropical environments, are arguments in favor of parthenogenesis which, under certain conditions, compensate for the inherent lack of genetic recombination to facilitate the rapid exploitation of newly colonized environments: a single isolated individual can generate a new population (Quintana et al., 2001-2002). The parthenogenesis and the exceptionally large size or large number of its offspring is typical of r-strategist populations (Dillon, 2000), although some authors have described *M. tuberculata* as a competitively superior k-adapted species (e.g. Pointier et al., 1991). The combination of characteristics summarized in this chapter (e.g. iteroparity, general purpose genotype, phenotypic plasticity, protection of breeding, flexibility in habitat requirements, apomitic reproduction, generalist diet, rapid population growth) has allowed this prosobranch to be a successful invader and to compete effectively with pulmonate snails (efficient strategists "r") in the conquest and occupation of freshwater environments and brackish water in many parts of the world. Introduction of the species into new areas and persistence in invaded aquatic systems could not only have a severe impact on native fauna and animal and human health, but also in altering the entire community structure and function (e.g. energy flow, primary production, and decomposition) of invaded ecosystems (Rader et al., 2003). As a consequence of the large invasive story of this species on the American Continent, mainly distributed as a result of the trade of aquarium plants, *M. tuberculata* could actually be considered as one of the most successfully introduced snail species in the New World.

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Chapter 4

CONE SNAIL BIOLOGY, BIOPROSPECTING AND CONSERVATION

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ABSTRACT

Cone snails are predatory marine gastropods that prey on worms, molluscs and fish. The venoms of these animals are true pharmacological treasures, and with the recent approval of the first cone snail venom-derived drug, the pressure on the resource is set to increase. While habitat loss and over-collecting for the shell trade are the major threat to cone snail diversity, every effort should be made to preserve this unique pharmacopoeia, including reducing to a minimum the number of specimens collected for scientific purposes. To this end, we show how recent improvements in sensitivity, miniaturisation of equipment, high throughput screens and novel technologies can help deliver valuable scientific and economic outcomes from small quantities of these limited samples.

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BIOLOGY, ECOLOGY AND CONSERVATION

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