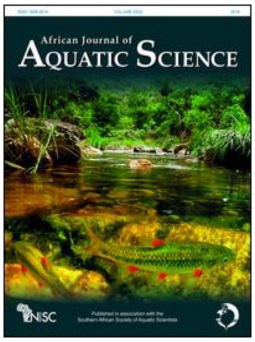

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# Alien and invasive fresh water Gastropoda in South Africa

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**Ten species of freshwater gastropod have been introduced into South Africa, mostly through the aquarium trade. Two of these, *Lymnaea columella* (Lymnaeidae) and *Physa acuta* (Physidae), have been invasive in river systems across the country for many years, probably since the 1940s or 1950s, and two recent arrivals, *Tarebia granifera* (Thiaridae) and *Aplexa marmorata* (Physidae), are spreading. Research on one of the well-established invaders, *P. acuta*, is reviewed and updated and a suite of attributes is identified that may have enabled it to become invasive.**

**Keywords:** alien, introduced, invasive, fresh water, gastropod, South Africa, *Physa acuta*

## Introduction

Research on introduced freshwater snails in South Africa has concentrated on the biology of species that have become invasive or which show the potential to do so, in an attempt to identify the attributes which enable such organisms to invade. An assessment of the state of knowledge of the ecological and economic consequences of the spread of these species was made by Ashton *et al*. (1986). The present contribution is an updated version of a review paper presented at the 2nd Workshop on Medical Malacology in Africa in Harare, Zimbabwe, in 1997 (Appleton and Brackenbury 1998). Its aims are (1) to update knowledge of the biology of invasive gastropods in South Africa, (2) to consider the invasive potential of several other species that are, at present, known only from artificial habitats, (3) to update what is known, or can be inferred from the literature, of the impact that these species might have on the systems they have colonised and (4) to present recent recommendations for the prevention and control of invasive species in South Africa.

## Alien gastropods in South Africa

Table 1 lists the four species of alien gastropod that are invasive or are becoming so in South Africa and a further six that have been introduced. Of these introduced species, five are known only from artificial waterbodies such as ornamental ponds, the aquarium trade and laboratories and one (*Helisoma duryi*) has become established in a number of natural habitats but has failed to spread.

The indigenous but widely distributed *Melanoides tuberculata* could be added to this list (see below). The Australian species *Physastra gibbosa* (Planorbidae) was reported as *Lenameria dispar*, the 'Australian red', by Barnard (1951) from aquaria and as *Physastra dispar* by Van Bruggen (1964) but has not been recorded since. The Asian planorbid *Gyraulus chinensis* was intercepted in a consignment of aquatic plants from the Far East by agricultural authorities in the 1980s (Brown *et al.* 1998) but has not been reported from within the country. No bivalves have been introduced into South Africa.

**Systematic list and notes on species** (see Appleton (1996) for further details)

### Prosobranchia
### Ampullariidae

***Pomacea bridgesii*** (Reeve, 1856) and ***P. lineata*** (Spix, 1827)

*Distribution in South Africa*: these two species are commonly sold by aquarium dealers in South Africa and are bred commercially within the country. Both may be found in ornamental ponds and *P. lineata* was collected in an impoundment on the Kloof River in Westville, Durban, by CD Dettman (Medical Research Council) in 1988.

*Status in other countries: Pomacea* spp., especially *P. canaliculata* (see below), have become invasive and reached pest status in rice paddies in several countries, viz. Japan (Yusa and Wada 1999), Taiwan (Cheng 1989), the Philippines (Litsinger and Estano 1993) and Hawaii (Cowie 1993).

*Vulnerable areas of South Africa:* based on the types of ecosystems invaded by *Pomacea* spp. in Asia and Hawaii, vulnerable environments in South Africa are the floodplains and swamps of the Pongolo and Mkuzi Rivers in north-eastern KwaZulu-Natal.

*Remarks:* both *P. bridgesii* and *P. lineata* are indigenous to

**Table 1:** List of alien freshwater gastropod species found in South Africa, with their status in South Africa and regions of origin

| Species | Status in South Africa | Region of origin | Main habitat types colonised |
|---|---|---|---|
| *Pomacea bridgesii* | non-invasive | South America | aquaria, ornamental ponds |
| *Pomacea lineata* | non-invasive | South America | aquaria, ornamental ponds |
| *Marisa cornuarietis* | non-invasive | South America | laboratories |
| *Tarebia granifera* | invasive | Asia | rivers |
| *Lymnaea columella* | invasive | North America | rivers, streams, ornamental and natural ponds |
| *Biomphalaria glabrata* | introduced | Caribbean, South America | laboratories |
| *Helisoma duryi* | non-invasive | North America | aquaria, ornamental ponds |
| *Planorbella* cf. *trivolvis* | non-invasive | North America | ornamental ponds |
| *Physa acuta* | invasive | North America | rivers, streams, ornamental and natural ponds |
| *Aplexa marmorata* | invasive | Caribbean, South America | ornamental and natural ponds |

South America and representative specimens were identified by Dra S Thiengo (Rio de Janeiro) and Dr T Berthold (Hamburg) respectively. *Pomacea lineata* is morphologically similar to *P. canaliculata* (Lamarck, 1822) such that Thiengo *et al.* (1993) recommended that the relationship between the two species should be investigated.

***Marisa cornuarietis*** (Linnaeus, 1758)
*Distribution*: specimens of Puerto Rican origin were introduced to laboratory aquaria in the 1980s to establish a colony for testing the species' suitability as a biocontrol agent against the snail hosts of schistosomiasis.

*Status in other countries: Marisa cornuarietis* has become invasive in Florida (Robins 1971) and several Caribbean Islands (Olivier-Gonzalez *et al.* 1956, Pointier *et al.* 1991, Vargas *et al.* 1991). In Africa it has become established in the Nile Delta, Egypt, and in irrigation canals in Sudan and Tanzania (Brown 1994). On the basis of its respiratory physiology (see below), it might be expected that the species would have spread from these irrigation schemes but there is no evidence that it has. Its use as a biocontrol agent in South Africa was not recommended (De Kock 1992).

*Vulnerable areas of South Africa*: a study of its respiratory physiology (Van Aardt and De Kock 1991) showed that *M. cornuarietis* is equipped to survive in heavily-vegetated, standing habitats which experience high temperatures, low oxygen tensions and occasionally high $CO_2$ levels as well. Its pigment haemocyanin has an unusually high affinity for oxygen, comparable to that of the haemoglobin in Planorbidae such as *Biomphalaria* and *Bulinus*. Measurements of the intrinsic rate of natural increase ($r_m$) over temperatures from 21°C to 30°C (De Kock 1992) showed that *M. cornuarietis* performed best at 27°C and that, if introduced, it might therefore be expected to spread over the sub-tropical eastern half of the country.

*Remarks:* an unmistakeable species that is native to the northern parts of South America. The large size and characteristic pattern of several dark, spiral bands on the shell are diagnostic features. It is the only discoid prosobranch snail reported from Africa.

### Thiaridae

***Tarebia granifera*** (Lamarck, 1816)
*Distribution*: this species is a recent introduction and appears to be spreading. To date it has been reported from two localities, a reservoir and a river, in KwaZulu-Natal (Appleton and Nadasan 2002, D Herbert pers. comm.) and a river in Mpumalanga (A Gerber pers. comm.). It was abundant at the two KwaZulu-Natal localities, approximately 1 000m$^{-2}$ in the reservoir and 'plentiful' in the river. Only a few specimens were collected at the Mpumalanga locality.

*Status in other countries*: *T. granifera* has become invasive on several Caribbean Islands, Venezuela and Florida.

*Remarks*: can be confused with the widespread indigenous thiarid *Melanoides tuberculata* but the shell is broader and the tubercles more prominent. It is an Asian species and as shown in Figure 1, the South African shells resemble Asian shells more closely than those from the Caribbean Islands. This suggests an Asian source of introduction which is consistent with the aquarium trade as agency. Hong Kong and Singapore are important sources of supply to the South African market.

## Pulmonata

### Lymnaeidae

***Lymnaea columella*** Say, 1817
*Distribution*: the species is invasive in southern Africa. It was first reported in 1942 at Somerset West near Cape Town (Brown 1994) but is now widespread across the sub-continent (Van Eeden and Brown 1966, De Kock *et al.* 1989, Anon. 1998), occurring in habitats as varied as artificial ponds, streams, rivers and lakes.

*Status in other countries*: it has become invasive in other southern African countries (Brown 1994) as well as Australia (Smith and Kershaw 1979), New Zealand (Pullan and Whitten 1972) and Brazil (Paraense 1983).

*Remarks*: *Lymnaea columella* is indigenous to North America. It can be distinguished from the indigenous lymnaeids by its elongate shape, well-developed spire, dark brown colour and reticulate sculpture. It is an amphibious species and its success as an invader in South Africa may

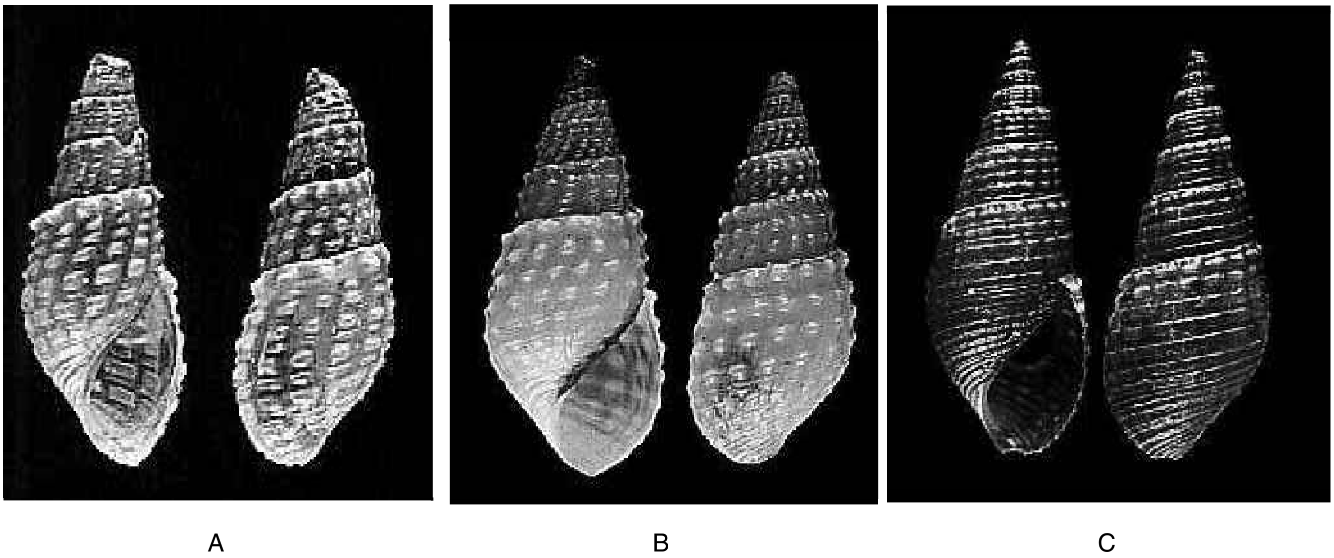

**Figure 1:** Photographs of *Tarebia granifera* from (A) South Africa, (B) Viet Nam and (C) Venezuela. The similarity between the shell sculpture of the specimens from South Africa and Viet Nam support an Asian origin for the South African material

be due in part to the absence of indigenous amphibious snails here. Remarkably little is known about this species in South Africa (see section on Economic impacts).

### Planorbidae

***Biomphalaria glabrata*** (Say, 1818)

*Distribution*: despite the warning by Pflüger (1982) of the possible consequences if allowed to escape, *Biomphalaria glabrata* was introduced into laboratories in South Africa in the mid-1980s for the maintenance of cultures of *Schistosoma mansoni*, the agent of human intestinal schistosomiasis. It has not been found outside these confines, although a large, discoid planorbid identified as *Biomphalaria* cf. *glabrata* was collected from ornamental ponds and a canal in central Durban during the 1980s. This snail was shown by Joubert *et al.* (1986) to be much less tolerant of low temperatures (0–6°C) than two widespread indigenous species, *Lymnaea natalensis* and *Bulinus tropicus*. It was also shown experimentally to be slightly susceptible to *S. mansoni* from Egypt and Israel (CHJ Schutte pers. comm.). Despite several searches, it has not been collected here in recent years.

*Status in other countries:* it has become established in parts on the Nile Delta in Egypt (Yousif *et al.* 1996).

*Remarks*: native to South and Central America and some Caribbean Islands. It grows to 40mm diameter, much larger than the indigenous *B. pfeifferi.* It may be confused with the next two species, *Helisoma duryi* and *Planorbella* cf. *trivolvis*, live specimens of which can be separated by the presence of an eversible holdfast (preputial) organ inside the preputium. *B. glabrata* is an efficient intermediate host for *S. mansoni.* According to Pflüger (1982), it has a broader ecological tolerance than the indigenous *B. pfeifferi*, but whether or not it has played a role in the recent rise in *S. mansoni* transmission in Egypt is unknown.

***Helisoma duryi*** (Wetherby, 1879)

*Distribution*: widespread but not invasive. It has been recorded from a number of artificial waterbodies across the country and one canalised river in Cape Town (Appleton 1977) as well as one natural stream in Mpumalanga (Evans *et al.* 1987). According to De Kock and Joubert (1991) there are 41 records for this species in the National Freshwater Snail Collection and that 15 (37%) of these are from 'natural' habitats, i.e. marshes, swamps, springs, rivers and streams. They note that although the earliest of these records was made 25 (now 36) years ago, there have not been any reports of geographic spread.

*Status in other countries*: known from many other countries but never as an invasive.

*Remarks*: *H. duryi* is indigenous to North America. It grows faster than indigenous planorbids such as *Bulinus africanus* and *Biomphalaria pfeifferi*, with higher fecundity rates and longer survival times as well (Joubert and De Kock 1989, 1990, De Kock and Joubert 1991). *H. duryi* has also been shown experimentally to interfere physically with other planorbids and reduce their fecundity rates (Madsen 1979). Joubert and De Kock (1989) concluded that, in terms of '$r_m$' measured at different temperatures, this species could colonise the warmer parts of South Africa, including the coastal lowlands of KwaZulu-Natal and the lowveld of Mpumalanga and Limpopo Province. It has also been introduced into other countries and become established in natural habitats in some cases but has never become invasive. This failure to invade has been attributed to its inability (De Witt and Sloan 1959, Madsen *et al.* 1983) or reduced ability (Paraense and Corrêa 1988) to self-fertilise. Single colonists will therefore be at a disadvantage since they will be unlikely to reproduce until copulation occurs and cross-fertilisation can take place. The biology of *H. duryi* has been extensively reviewed by Madsen (1992).

***Planorbella* cf. *trivolvis*** (Say, 1817)
*Distribution*: this species has been known from artificial canals and ponds within the Durban Metropolitan Area since the 1960s (J Agnew pers. comm.) but has not spread. Representative specimens were identified by Dr JB Burch (University of Michigan). Recent attempts to find this snail have failed.

*Status in other countries*: none known.

*Remarks*: following J Agnew (pers. comm. 1987), an unidentified, discoid planorbid had been known from artificial waterbodies in the Durban Metropolitan Area since the 1960s. Whether this species was *P.* cf. *trivolvis* or that identified as *Biomphalaria* cf. *glabrata* (see above) is not known but, whatever their true identities, neither has spread and recent attempts to find either of them have failed.

**Physidae**
***Aplexa marmorata*** (Guilding, 1828) (Figure 2a)
*Distribution*: this species was collected from a pond in a nursery in Pinetown, Durban, in 1986. Shortly afterwards it was reported from other localities within the Durban Metropolitan Area and an artificial pond in Tzaneen (Limpopo Province, formerly Northern Province) (Appleton *et al*. 1989). Subsequently it has been collected in a backwater in the Sabie River in the Kruger National Park (Mpumalanga) by De Kock and Wolmarans (1998). It is now widespread in the Durban area and has also been found at several localities on the south and north coasts of KwaZulu-Natal (CC Appleton unpublished data). Anecdotal evidence suggests that the Tzaneen population was translocated from either south-east Zimbabwe or adjacent area of Mozambique (Appleton and Brackenbury 1998).

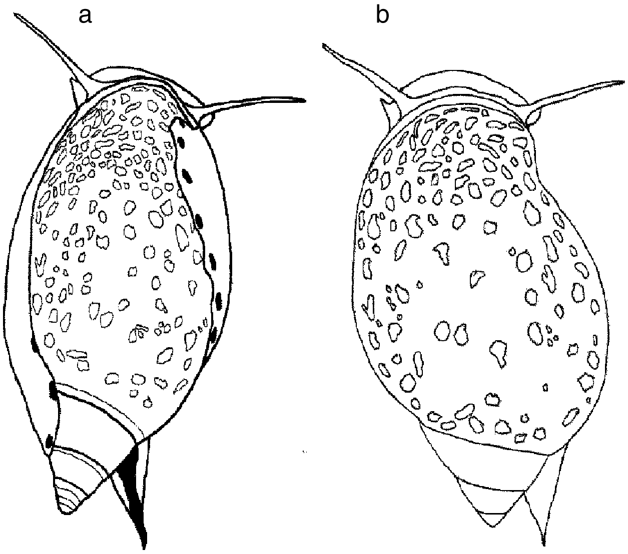

**Figure 2:** Life drawings of (a) *Aplexa marmorata* and (b) *Physa acuta* from above. Note that in both species, the mantle markings can be seen through the shell. The shell of *A. marmorata* is more elongate and less broad than in *P. acuta*, the mantle flaps extend further over the shell, a 'sutural band' is visible and the tail has a median black stripe

*Status in other countries:* it has been well established in West Africa since early in the 20th century (and probably much longer).

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*Remarks*: native to South America and some Caribbean islands. There is no doubt (Dana 2000, WL Paraense pers. comm., CC Appleton unpublished data) that the South African populations of *A. marmorata*, *A. waterloti* from West Africa (see Brown 1994) and the 19th century record of *Physa mosambiquensis* from Mocambique (Connolly 1939) represent the same species. Uncertainty remains however as to whether this species belongs in the genus *Aplexa* as suggested by Appleton *et al.* (1989), Brown (1994) and Dana (2000) or in *Physa* as maintained by Paraense (1986).

***Physa acuta*** Draparnaud, 1805 (Figure 2b)
*Distribution*: this species was first reported from South Africa in the Umsinduzi River, Pietermaritzburg, in 1954 (KN de Kock pers. comm.) and during the intervening decades has spread and colonised many of the country's river systems (Hamilton-Attwell *et al.* 1970, De Kock *et al.* 1989). The maps given by the above authors show clusters of records around the major urban centres, especially ports, suggesting that several introductions may have occurred.

*Status in other countries*: invasive in many countries in Africa as well as Europe, Australia and parts of Asia.

*Remarks*: although described from France in 1805, evidence is growing that *P. acuta* is conspecific with a suite of species from the eastern states of North America such as *P. cubensis*, *P. heterostropha* and *P. integra* (Te 1978, Dillon *et al.* 2001, Wethington *et al.* 2001, WL Paraense pers. comm.). If this is confirmed, *Physa acuta* is the oldest name and will therefore be maintained. In 1986 it was the most abundant gastropod in the Umsinduzi River, Pietermaritzburg, at ratios to indigenous species of between 2:1 and 17:1 in different parts of the river (n = 10 samples) (AFG Tonin unpublished data). It has also been recorded in Namibia and Zimbabwe (Curtis 1991, BE Marshall, University of Zimbabwe, pers. comm.) and was recently collected in Lake Kariba (Anon. 1998).

## Sources of introduced snails

In their review of introduced freshwater snails worldwide, Madsen and Frandsen (1989) noted that the most commonly found invasive species belong either to the Thiaridae or to the Pulmonata which presumably relates to their modes of reproduction: the Thiaridae are parthenogenetic and the pulmonates are hermaphrodites. Species of *Pomacea* could be included, particularly for Asia where they colonise specific types of habitat, e.g. rice paddies.

They stressed that the aquarium trade was probably responsible for distributing several common species and listed six species imported into Denmark with fish and plants, seven found in aquarium shops in Sao Paulo, Brazil (Corrêa *et al.* 1980) and five in consignments arriving at Sydney Airport, Australia (Walker 1978). I have found six species in aquarium shops in Durban, South Africa: *Pomacea bridgesii*, *P. lineata*, *Melanoides tuberculata*, *Lymnaea natalensis, Helisoma duryi* and *Physa acuta*. *Melanoides tuberculata* and *L. natalensis* are indigenous species.

The introduction of at least six of the species discussed in the section above into South Africa was probably via the aquarium trade, viz. *Pomacea bridgesii, P. lineata, Tarebia granifera, Helisoma duryi, Physa acuta* and *Lymnaea columella*. Two others, *Marisa cornuarietis* and *Biomphalaria glabrata*, were introduced for scientific research purposes and it seems possible that *Aplexa marmorata* has been present in south-eastern Africa for at least 160 years, perhaps having been introduced via the Portuguese slave trade (Appleton *et al.* 1989). The source of *Planorbella* cf. *trivolvis* is not known. *Melanoides tuberculata* is also distributed by the aquarium trade and is commonly found in aquaria in South Africa. Although indigenous to Africa, it is distributed over a wide area including India, parts of Asia and northern Australia. It seems probable that stock imported with aquarium supplies from Asia has been introduced and, even though most individuals are parthenogenetic females, males do exist (Hodgson and Heller 1990) and may have interbred with indigenous snails.

## Distribution of invasive snails

Maps of the distribution of invasive snails in South Africa, both terrestrial and freshwater (Van Bruggen 1964, Hamilton-Attwell *et al.* 1970, De Kock *et al.* 1989), have all shown a common pattern of accumulations of records around the major ports from Cape Town to Durban and to a lesser degree, inland cities as well. A comparison of data presented for freshwater species by Van Eeden and Brown (1966), Hamilton-Attwell *et al.* (1970) and De Kock *et al.* (1989) shows that the two longest-established species, *Lymnaea columella* and *Physa acuta*, have expanded their ranges considerably over the ±20 years between the late 1960s and the late 1980s and are probably continuing to do so. In fact, as Brown pointed out in 1994, *L. columella* has become the third most widely distributed freshwater pulmonate in South Africa, a feat that presumably reflects a broad temperature tolerance and its amphibious habit. *Lymnaea columella* occurs along the entire coastal strip from the south-western Cape to the KwaZulu-Natal/Mozambique border as well as most of inland KwaZulu-Natal, the Vaal/Gariep River system except for the extreme eastern parts, and most of Mpumalanga, Northern and North-West Provinces. *Physa acuta* is less widespread, being known from the middle reaches of the Vaal/Gariep system, Gauteng, much of KwaZulu-Natal and the extreme south-western Cape. The two newly invasive species, *Tarebia granifera* and *Aplexa marmorata*, appear limited to the subtropical areas of KwaZulu-Natal and Mpumalanga but both are spreading and need to be monitored.

## Impact of invasive snails on colonised habitats

The severest impacts due to invasive freshwater molluscs anywhere have been by bivalves but, as noted above, there are no invasive bivalves in South Africa. In addition, no attempts have been made to assess quantitatively the effects that invasive snails in South Africa have had on waterbodies they have colonised. It must, however, be naïve to think that they have not had any impact, especially where population densities are high, e.g. ±3 000m$^{-2}$ for *P. acuta* (Brackenbury and Appleton, 1993) and ±1 000m$^{-2}$ for *T. granifera* (Appleton and Nadasan 2002).

## Ecological impacts

Freshwater snails are microphagous feeders (grazers) whose diet includes a variety of food items in the periphyton such as detritus and algae on submerged surfaces and decaying plant tissue. This food resource is shared with indigenous grazers such as other snails and some insects and when invasive snails reach high densities, they must surely reduce the food available to the indigenous grazing invertebrates. SEM examination of decaying leaves of *Bridelia micrantha* grazed by *T. granifera* showed (Figure 3) that these snails have grazed them from the undersurface, working through the lower cuticle, epidermis and spongy mesophyll to expose the vein network. Little bacterial or algal growth was seen on these leaves (see under 'Feeding' below).

In high-density situations, physical interactions between invasive snails and indigenous invertebrates may also be important. For example, laboratory observations (Madsen 1979, 1992) have demonstrated that physical interference between *Helisoma duryi* and other planorbids resulted in fewer egg masses as well as reduced hatching and slower growth rates in the other species. In this respect it is useful to consider the consequences of invasion elsewhere by fresh water molluscs, in some cases the same species that are present in South Africa. For example Pointier (1999) details the effects of invasion by *T. granifera* in Puerto Rico, Cuba and Venezuela. In each case it reached high population densities and was associated with the disappearance of the indigenous species *Biomphalaria glabrata* (Planorbidae) in affected habitats in Puerto Rico and Venezuela and *Pachychilus violaceus* (Pleuroceridae) in Cuba.

The prosobranch snail *Melanoides tuberculata* (Thiaridae), native to Africa and south-east Asia, is also having an impact in South and Central America where it is widespread. It threatens to cause the extinction of an indigenous species. *M. tuberculata* resembles the indigenous thiarid *Aylacostoma choroticum* morphologically but, according to Quintana *et al.* (2000), differs markedly in reproductive output. The former lives for 2–3 years, produces ±63 juveniles/brood and releases 0.5–2 juveniles day$^{-1}$; each adult eventually giving rise to about 500 adults year$^{-1}$. It is thus strongly 'r-selected' in contrast to *A. choroticum* which is 'K-selected', also taking 2–3 years to mature but producing very few, though large, young at a time. Quintana *et al.* (2000) believe that *M. tuberculata* is too 'aggressive' a com-

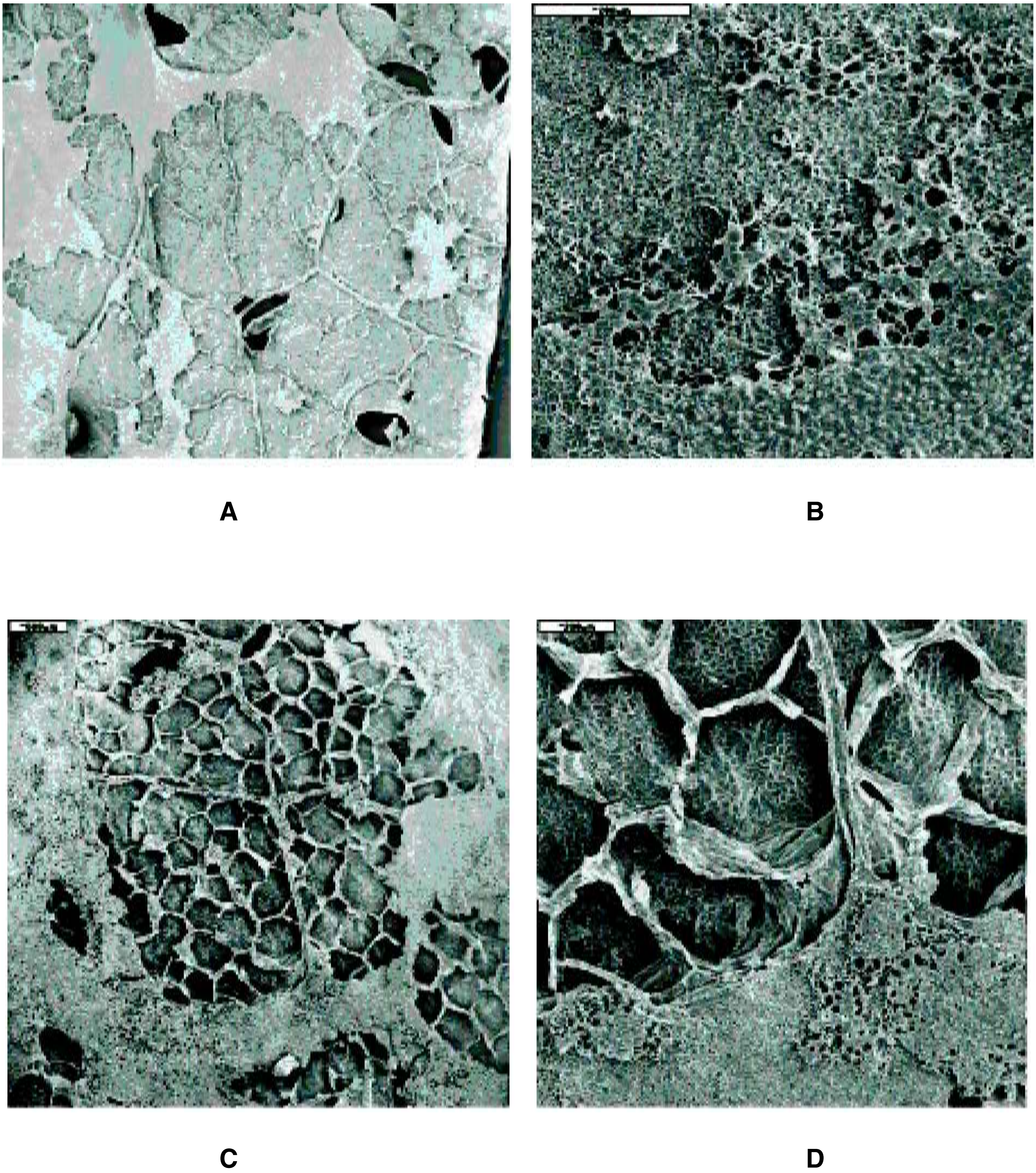

**Figure 3:** Scanning Electron micrographs showing the effects of grazing by *Tarebia granifera* on the undersurface of a decaying leaf of *Bridelia micrantha*; (A) shows a low magnification (23x) view of the undersurface of the leaf with the cuticle, epidermis and spongy mesophyll exposed to show the veins; (B) shows a 200x view of the epidermis removed to expose the spongy mesophyll; (C) shows a 30x view of exposed veins protecting the pallisade mesophyll and upper epidermis layers and (D) shows a 100x view of the exposed veins with some spongy mesophyll and epidermis still intact

petitor for *A. choroticum* to withstand and that the latter is seriously threatened and will probably become extinct within the next 10–20 years. They thus stress the need to develop methods for the artificial culture of threatened species like *A. choroticum*. In the South African context, *Tarebia granifera* is also r-selected, parthenogenetic and appears to have been introduced more than once. Apart from *M. tuberculata*, there are few bottom-dwelling gastropods in South African rivers but in situations where it reaches high densities, *T. granifera* may reduce the diversity of other indigenous benthic invertebrates.

## Economic impacts

Two invasive snail species have had serious economic consequences in areas they have colonised, particularly in Asia. Although economic costs are usually difficult to assess, a detailed analysis of the costs of the invasion of rice paddies in the Philippines by the 'apple' snail *Pomacea canaliculata* was made by Naylor (1996). She estimated that the cumulative cost to farmers from 1980, when *P. canaliculata* is believed to have been introduced, to 1991 was (at 1991 rates) US$425 million. In Japan Yusa and Wada (1999) showed that *P. canaliculata* has expanded its range each year and had colonised between 50 000ha and 60 000ha of rice paddies by 1998, with damage to about 3 000ha (i.e. ±6%) but they did not estimate the costs involved.

*Lymnaea columella* serves as intermediate host for *Fasciola hepatica* in Australia (J Boray pers. comm.) and New Zealand (Harris and Charleston 1976). Indeed, according to Pullan and Whitten (1972) the prevalence of fascioliasis in New Zealand has increased since the introduction of *L. columella.* According to Van Eeden and Brown (1966) and Reinecke (1983), *L. columella* is susceptible to both species of liver flukes infecting livestock in South Africa, *F. hepatica* and *F. gigantica*, but there seems to have been no confirmation of its epidemiological role as an intermediate host. Indeed, it appears that not all South African *L. columella* populations are susceptible to *F. hepatica* (J van Rensburg pers. comm.).

## Biology of *Physa acuta*

Research on invasive freshwater gastropods in South Africa has concentrated on the biology of *Physa acuta* — a species that has become invasive on four continents. This work is reviewed in the context of research on other physids, mostly in North America, including those species (*P. cubensis, P. heterostropha* and *P. integra*) thought to be conspecific with *P. acuta*. Using this comparative approach, differences in biology and ecological requirements between *P. acuta* and the common indigenous pulmonates of the family Planorbidae are exposed in the hope that they will help identify attributes that have enabled *P. acuta* to become invasive.

### *Population dynamics*

Freshwater pulmonates typically undergo an annual lifecycle with a single breeding season (univoltine) but there is evidence that at least some members of the Physidae are able to live longer and have more than one breeding period. Physids usually live for slightly more than a year, i.e. 12–15 months but up to 18–20 months in seasonal habitats, depending on the length of the dry phase. Some species are bi- or even multivoltine (Brown 1979).

*Physa acuta* differs from other physids whose bionomics have been investigated in that it is a short-lived, adaptable species with a life cycle that is more 'plastic' than others. Duncan (1959) reported that in Europe the species was univoltine, breeding in spring in natural habitats such as rivers but may become bivoltine in artificial habitats such as reservoirs and canals receiving effluent, producing a smaller second generation in late summer. Perrin (1986) confirmed the species' short life cycle in the laboratory, showing that only 50% of European snails lived longer than 17–18 weeks, that reproductive maturity was reached in five weeks and that adults died soon after egg-laying had ceased. He categorised *P. acuta* as having a 'mixed reproductive strategy', varying between univoltine and bivoltine. Jambari (1993) reported that Malaysian *P. acuta* were also short-lived (not longer than 17 weeks) and matured at ±5 weeks (at 27°C). However they produced an average of 2 635 eggs/snail over a reproductive life of ±12 weeks which equates with an average output of 220 eggs/snail/week — far higher than the 41.3 eggs/snail/week given for South African snails measured over a range of temperatures by Brackenbury and Appleton (1991). In addition, Jambari (1993) reported an average clutch size of 102 eggs (at 27°C) and an incubation period of 4–6 days. The corresponding data for South African *P. acuta* are a clutch size of 6–69 eggs (mean 28.0) and an incubation period varying according to temperature from four to 15 days (Brackenbury and Appleton 1991). The much higher clutch size of Malaysian snails may reflect the constant 27°C used by Jambari (1993).

A histological study of gametogenesis in laboratory-bred South African snails (Brackenbury and Appleton 1991) showed no evidence of a bivoltine reproductive pattern but the field study by Brackenbury and Appleton (1993) reported repeated breeding by *P. acuta* following successive floods in the Umsinduzi River, Pietermaritzburg, KwaZulu-Natal, during the exceptionally heavy 1987/1988 rainy season. Oviposition rates were not monitored. In a study of *P. integra* (considered to be synonymous with *P. acuta* — see above), Clampitt (1970) in the USA reported that, like *P. acuta*, it produced two generations, one in early summer and the other in early autumn, and also that there was a high mortality of older snails shortly after egg-laying activity stopped.

The study by Brackenbury and Appleton (1993) provided a useful demonstration of the reproductive adaptability of a species that normally exhibits a univoltine pattern in its native areas. *Physa acuta* produced seven cohorts at intervals of 1–3 months, each after a flood, and became the dominant gastropod in the river each time. The first sample (1/2/88) demonstrated that, five months after the flood in September 1987, *P. acuta* was the only snail species to have recolonised the river and was abundant at 507 ± 185m$^{-2}$. This population disappeared following a second flood in March 1988 which reached flow rates approaching 16m$^3$s$^{-1}$. It remained low during the winter and in spring (August–October) increased to nearly 300m$^{-2}$. A third flood in

October 1988, which reached $4m^3s^{-1}$, reduced *P. acuta* numbers by ±80% and a fourth flood in November/December 1988 removed the remaining snails. The species had not returned by the end of January 1989 when sampling stopped but a visit to the site in March 1989 showed *P. acuta* to be abundant once again.

The seven successive cohorts were delineated using Harding's (1949) polymodal analysis technique. The production of this many cohorts within a single rainy season and the high population densities attained each time imply rapid maturation by *P. acuta* coupled with high fecundity rates. Egg capsules with a mean clutch size of 33.0 ± 18.8 eggs (n = 50) were laid mostly on rock and compacted mud at densities ranging from 100–4 477 capsules $m^{-2}$ throughout the year. Up to 42% of adult *P. acuta* sampled had 1–6 egg capsules laid on their shells. Similar size-dependent carrying of egg capsules was also recorded for 29% of adult *P. cubensis* (>9mm) in Brazil (CC Appleton unpublished data 2000).

By comparison, two of the other pulmonate species that were present in the Umsinduzi River prior to the September 1987 flood also re-established themselves but took longer. *Bulinus tropicus* (Planorbidae) appeared sporadically at densities of $41–57m^{-2}$ in June 1988 after the marginal vegetation had started to return. The other pulmonate, *Lymnaea columella* (Lymnaeidae), also an invasive, only re-appeared in September 1988, a year after the initial flood, at densities of $54–66m^{-2}$. No other snail species were found at the study site (Grimthorpe) during the study period.

Like many watercourses subject to biological invasion, the Umsindusi River has been disturbed not only by floods but also by flow regulation and pollution. Floods altered the physiognomy of the river repeatedly during 1987/1988 yet *P. acuta* was able to re-colonise the scoured bed each time (Brackenbury and Appleton 1993). While the effect of these flood events on the snail community was marked, it was relatively short-term in the case of *P. acuta*. This species returned each time to comprise between 80–100% of the gastropods present whereas the most common indigenous species, *B. tropicus*, never exceeded 20%. The ability of *P. acuta* to produce seven consecutive cohorts of offspring in quick succession in response to repeated flooding in a South African river demonstrates a tolerance of habitat instability. To what extent this pattern of repeated breeding was a consequence of the repeated disturbance of the environment is not clear since *P. acuta* clearly has a short life-cycle, i.e. less than six months (Perrin 1986, Jambari 1993). The ability of *P. acuta* to survive stressful conditions, and even to capitalise on them, was demonstrated experimentally by Krkač (1982). Juvenile and young adult snails were shown to survive sudden increases in temperature (thermal shock) across a wide range of acclimation temperatures with low (less than 32%) mortality. Older adults (>11mm) showed greater mortality (up to 68%), especially at low acclimation temperatures (5°C). However, all mature *P. acuta* responded to such temperature increases (5–15°C) by laying eggs.

In the southwestern USA, Thomas and McClintock (1996) found that the life-cycle of *P. cubensis* (now thought to be synonymous with *P. acuta* — see under '*Physa acuta*' above) was also influenced by habitat stability. In a permanent stream the pattern was dictated by temperature and rainfall while in a nearby seasonal pond it was dictated by episodic drying events. In the stream, snails of all sizes became inactive and aestivated in the sediments for up to 7½ months during winter. Numbers of active snails declined rapidly to zero after the water temperature fell below about 15°C and increased again as temperatures rose above this level in late spring. In the pond only juveniles <5mm shell height aestivated successfully in the dried sediments, and did so for up to 5½ months. Drying caused heavy mortalities amongst larger, adult snails.

Species of *Physa* also differ from the second invasive physid in South Africa, *Aplexa marmorata*, in respect of the types of habitat they colonise. *Physa acuta* and *P. cubensis* are found in both flowing and standing habitats while *A. marmorata* is normally found in standing waterbodies — rarely in flowing watercourses (CC Appleton unpublished observations in South Africa and Brazil). Dana (2000) concluded from a field study in Durban, South Africa, that *A. marmorata* had a cycle of 14–15 months. She estimated that reproductive maturity was attained at a shell height of 6–7mm, i.e. at an age of about seven months, but this estimate may be conservative and was not based on histological evidence. Data on reproduction did not allow the identification of a breeding season.

Other biological attributes may play a role in the process of spread from founder populations in a new environment. These are considered below.

### *Feeding*

Not only are the teeth of physid snails arranged in chevron-patterned rows and not in parallel rows as in lymnaeids and planorbids but they have more cusps per tooth and these cusps are longer and sharper than in the other two families. Kesler *et al.* (1986) detailed many features of the alimentary system of *Physa vernalis* and pointed out that the physid jaw is non-opposable, so that food cannot be pushed up against the jaw by the radula and bitten off. Also, individual teeth are designed to lock together in position on the radula and the long, pointed cusps may be used for piercing food as well as scraping. Using video recordings, Appleton and Brackenbury (1998) demonstrated that the actual feeding mechanism, i.e. movement of the radula, of *Physa acuta* was very different from that of the indigenous *Bulinus tropicus*. Kesler *et al.* (1986) also noted that the stomach of *P. vernalis* was thin-walled and simpler in structure than the stomachs of lymnaeids and planorbids and rarely contained sand grains — a feature also listed by Reavell (1980) for *P. fontinalis*. Kesler (1983) reported relatively low levels of cellulase activity in *Physa heterostropha* and suggested that this species could not digest algal cells as efficiently as lymnaeids which have higher cellulase levels.

Data on the diet of physids are however scarce. Kesler *et al.* (1986) categorised *P. vernalis* as a detritivore whereas *L. columella* was classed as an omnivore, consuming more algal filaments than the physid. Although the stomach contents of both species were dominated by detritus and diatoms, this was more so in *P. vernalis.* This species was also observed to avoid stands of filamentous Chlorophyta such as *Cladophora, Oedogonium* and *Spirogyra*, apparently because it cannot crop the filaments as efficiently as lym-

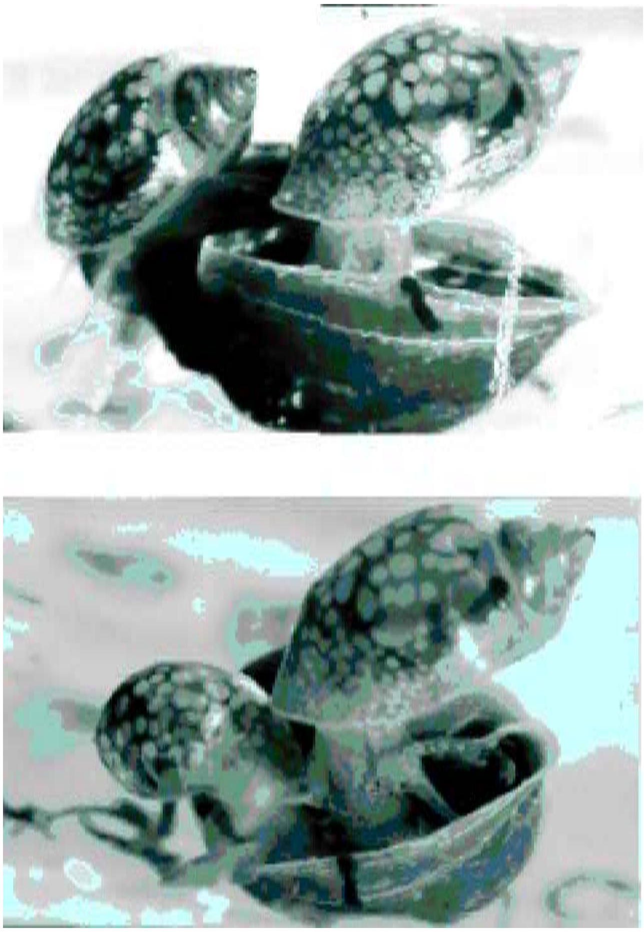

**Figure 4:** Photographs of two *Physa acuta* apparently attacking an adult *Bulinus africanus*

naeids can (see Clampitt 1970, Lodge 1986), presumably as a consequence of the non-opposability of its jaw and radula. Animal parts are seldom found in the stomachs of physids but Figure 4 raises the possibility that *P. acuta* may be carnivorous or a scavenger on occasions.

In the Umsinduzi River *P. acuta* is common on the sandy substratum in flowing water in mid-channel and the stomach contents of 20 snails from this habitat at Pietermaritzburg comprised mostly frustules of the same diatom species which coat the sand grains here (Brackenbury 1989). When viewed under the SEM, the diatom flora on the sand comprised predominantly *Nitzschia* and *Navicula* spp. with occasional *Cyclotella* and *Rhizosolemia* spp. giving a density of 850 diatoms mm$^{-2}$ to 1 024 diatoms mm$^{-2}$ (n = 2). *P. acuta* is also common on rocks at the channel edge where it feeds on a more varied resource, the periphyton.

Assuming that the morphological features described above for the alimentary systems of *P. vernalis* and *P. heterostropha* are common to other members of the Physidae, they set the family apart from the other Basommatophora in African fresh waters and presumably reflect differences in feeding and diet between the two groups. Extensive grazing by dense populations of invasive physids may therefore have an adverse effect on the food resources available to other microphagous grazers in invaded habitats.

### *Locomotion*

In North America physids are known to move more rapidly than planorbids over sandy substrata (Clampitt 1970, 1973) and in South Africa Brackenbury (1989) showed that this applied to *P. acuta* and its common indigenous planorbid counterpart, *Bulinus tropicus*, as well. When compared to the slow meanderings with high a turning rate of *B. tropicus*, *P. acuta* exhibited more rapid, directional locomotion. While *B. tropicus* moved within a confined area of a few square centimetres around its starting point, *P. acuta* foraged more widely. Brackenbury (1989) interpreted the confined movement of *B. tropicus* as reflecting the association of planorbids with aquatic vegetation (Lodge 1985, Van Schayck 1985) whereas for *P. acuta*, rapid, directional movement indicated an adaptation to foraging on more exposed and uniform substrata such as the sediments of lakes and streams in which many physids live in their native North America (Clampitt 1970, 1973) and independence from macrophytes. Bay *et al.* (1998) demonstrated a similar high turning-rate locomotory pattern for another planorbid, *Biomphalaria glabrata*, around a food source. In terms of velocity, *P. acuta* moved 3½ times faster than *B. tropicus*, i.e. 1.34 ± 0.1mm s$^{-1}$ and 0.39 ± 0.17mm s$^{-1}$ respectively (n = 60 in both cases) (Appleton and Brackenbury 1998).

### *Current velocity*

*Physa acuta* is tolerant of faster current velocities than its indigenous counterparts. Measurements made by placing the probe of a Marsh McBirney 201 Flowmeter as close as possible (19mm) to *P. acuta in situ* on rock in the Umsinduzi River showed that it was tolerant of velocities up to 0.6m s$^{-1}$ whereas *B. tropicus* and other indigenous pulmonates are not known to occur in water flowing faster than 0.3m s$^{-1}$ (Appleton 1978). This higher current velocity tolerance, and an apparent lack of any association with the marginal vegetation, allows *P. acuta* access to more of the available substratum than the indigenous snails.

### *Parasitism*

Host specificity will generally preclude invasive molluscs from serving as first intermediate hosts in trematode life-cycles in their adopted countries. Exceptions are unlikely except where the parasite is also introduced, e.g. *Lymnaea columella* and *Fasciola hepatica* in New Zealand (Pullan and Whitten 1972) (see section on Economic impacts). Trematodes are less host specific with regard to their second intermediate hosts and introduced species do become involved here. Thus, none of 594 *P. acuta* examined from the Umsindusi River had prepatent or patent trematode infections but 11.3% harboured metacercarial cysts of echinostome flukes (Echinostomatidae) in their pericardial sacs (Appleton and Brackenbury 1998).

### *Predation*

Nothing is known of predation on *P. acuta* in its adopted habitats though Wilken and Appleton (1991) have shown experimentally that it is significantly less susceptible to attack by the indigenous, malacophagous leech *Helobdella conifera* than several indigenous species including *B. tropicus*. Appleton *et al.* (1993) obtained similar results using the larvae of the indigenous sciomyzid flies, *Sepedon neavei* and *S. scapularis*. It is however just as susceptible to attack by the waterbug *Appasus grassei* as the indigenous species (Baijnath 1999).

Success in avoiding capture by slow-moving predators such as *H. conifera* and *Sepedon* spp. larvae is due largely to the ability of *P. acuta* (and also *A. marmorata* although less is known about this species) (i) to move more rapidly than indigenous snail species and (ii) to prevent the predator from gaining a firm hold on its shell. The latter is achieved by executing avoidance manoeuvres (Wilken and Appleton 1991) including flicking its shell rapidly sideways on its foot. This is an ability of many, if not all, Physidae and is facilitated by the possession of a unique set of muscles called the 'physid musculature' by Harry and Hubendick (1964). The anatomy of this musculature is complex but one of its main branches is wrapped around the columellar muscle with the result that on contraction it uses the latter as a pivot, pulling the shell in a clockwise arc as it does so (E Naranjo-García and CC Appleton unpublished data).

## Discussion

Studies on the reproductive biology of *P. acuta* in different parts of the world have shown that the species has a high fecundity rate which, in the South African context at least, gives it a reproductive advantage over several common indigenous pulmonates (Appleton and Brackenbury 1998). This advantage is conferred by earlier maturation (i.e. precocious development), larger egg size, higher egg-output, shorter incubation period and mean generation time and a greater responsiveness in terms of gametogenesis to changing temperatures than, for example the indigenous *B. tropicus*. The precocious development referred to above may be explained by the finding of Thomas and McClintock (1990) that *P. cubensis* (thought to be synonymous with *P. acuta*) lacks a veliger stage while this stage is present in the non-invasive physid, *P. gyrina* (De Witt 1954). Absence of a veliger stage may result in embryogenesis reaching completion more quickly.

In the field situation, these attributes manifest themselves as rapid doubling times and the ability to switch between univoltine, bivoltine and even multivoltine patterns. Reproductive patterns were reviewed earlier but doubling times calculated from data given by Brackenbury (1989) ranged from 4.1 weeks at 15°C to 2.1 weeks at 28°C as opposed to 9.2 weeks to 3.7 weeks respectively for *B. tropicus*. Perrin (1986) cited a doubling time (at 20°C) of 'aproximately four weeks' for *P. acuta* from France. These doubling times derived for *P. acuta* from experimental data compare well with those calculated from the Umsindusi River sampling results (Brackenbury and Appleton 1993) and suggest that those constraints which were eliminated in the laboratory, e.g. predation and parasitism, or which were present in excess, e.g. food, may also apply to the invaded environment. In such habitats *P. acuta* probably (i) experiences little in the way of mortality due to predation, (ii) maintains a high level of fecundity unaffected by patent trematode infections (this can exceed 75% in some planorbids (D Nadasan unpublished data) or temperature and (iii) has access to an abundant food supply.

These attributes are of course coupled with others such as fast growth and development, small adult size, short lifespan, high density-independent adult mortality, rapid locomotion, tolerance of current velocities >0.3m s$^{-1}$, a catholic diet, reduced parasitism and successful avoidance of slow-moving predators. Together they have equipped *P. acuta* to colonise both lentic and lotic habitats by surviving stochastic events such as periods of drought, frequent and severe floods and sudden increases in temperature. In addition, *P. acuta* appears to lack the association with submerged vegetation shown by other pulmonates (Pip and Stewart 1976, Lodge 1985, Van Schayck 1985, Thomas 1987). This, as demonstrated by the Umsinduzi River study of Brackenbury and Appleton (1993), allowed *P. acuta* to recolonise the river before the indigenous species such as *Bulinus*. Field studies on the population dynamics of *P. acuta* in permanent, stable habitats are needed.

*Physa acuta* has acquired the nick-name of 'the sewage snail' and in the Umsindusi River it is often the only mollusc living in water with faecal contamination producing high *E. coli* counts. Records from the vicinity of the Grimthorpe site (see Brackenbury and Appleton 1993) show a background level of <1 000 100ml$^{-1}$ but rising intermittently (especially in summer) to as much as 70 000 100ml$^{-1}$ on occasions (I Bailey unpublished data). Brown (1994) commented that in Africa *P. acuta* was often collected in obviously polluted water and seemed to have difficulty in establishing itself far from human works or habitation. Jambari (1993) agreed and emphasised that in Malaysia, *P. acuta* was tolerant of habitats 'slightly' contaminated with 'domestic-derived pollutants'. In Europe Alexandrawicz (1986) associated the species' spread across the continent with that of polluted and heated waters due to industrial expansion. These attributes seem likely to have helped it colonise disturbed habitats and *Physa acuta* may have become, like other invasives, a species associated with man.

### ***Prevention and control of introduced freshwater molluscs***

In 2000 the South Africa/United States of America Bi-national Commission held a symposium to consider the best ways of preventing the introduction of aliens and, for those already introduced, realistic methods of controlling them (Preston *et al.* 2000). Measures identified for freshwater invertebrates were summarised by Appleton and Bosman (2000) and several important points are listed below:

Cost-effective prevention of the introduction of potential invasive organisms rests on a legal framework allowing interception at the point of entry. This already exists in South Africa but it should be improved by:

1 The compilation of a list of potentially invasive molluscs, including aquarium species, and updating this regularly in accordance with national and international experience, e.g. Ridgeway *et al.* (1999). This could then be used to develop a risk assessment process and an early warning system, e.g. sections I–IV of the ICES Code of Practice

(ICES 1995) and Risk Assessment and Management Committee (1996).

2 Larger budgets to improve the efficiency of the interception process at points of entry, including ongoing training and refresher courses for officials/inspectors examining incoming cargoes so as to be able to recognise potentially invasive species.

3 Increased public awareness of the harmful effects that invasive freshwater molluscs can have on their adopted environments. This includes the education of schoolchildren. The public should be made aware that (i) harbouring potentially invasive or invasive molluscs may be illegal and (ii) that, as introducers, they may be liable for the costs of control.

Two invasive species, *L. columella* and *P. acuta,* are too widespread for any control programme be cost-effective and both of the recently introduced species, *T. granifera* and *A. marmorata*, are spreading though the latter is more widely distributed than the former. *Aplexa marmorata* has in fact been collected at some remarkably remote localities in KwaZulu-Natal (CC Appleton unpublished data) where human agency can probably be discounted as a mechanism of distribution. Attempts should be made however to monitor species of *Pomacea*. These are large snails and should be easily seen. Established populations, provided they occur in only a restricted area, could be controlled using a molluscicide such as metaldehyde or perhaps manual-collecting (Cheng 1989, Litsinger and Estano 1993).

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