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Re-examination of *Physa mosambiquensis* Clessin, 1886 and its relationship with other Aplexinae (Pulmonata: Physidae) reported from Africa

by

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ABSTRACT

Physa mosambiquensis Clessin, 1886 (Physidae) has long been an anomaly in the freshwater malacology of southern Africa. The type specimens and all available literature records are examined and used to propose an area of origin for the species and a mode of translocation to Africa. It is concluded that *P. mosambiquensis* is conspecific with *P. marmorata* from South Africa and *P. waterloti* from several west African countries (both were previously assigned to *Aplexa* by some authors), and that all these African Aplexinae conform to the South American *P. marmorata* (sometimes ascribed to *Stenophysa*). The spread of *P. marmorata* in eastern South Africa is updated.

KEY WORDS: Pulmonata, Physidae, Afrotropical, Neotropical, freshwater snail, invasive species, synonymy.

INTRODUCTION

Clessin (1886) described *Physa mosambiquensis* from specimens of a physid snail collected in Mozambique by Wilhelm H. Peters between 1842 and 1848. According to Von Martens (1879) the collection dates were between 1843 and 1847. Recognising that these snails differed from the usual African freshwater gastropod fauna, Clessin (1886) noted that they resembled South and Central American species more than they did East African species. The fact that the family Physidae is not indigenous to the Afrotropical Region has meant that this very early record of *P. mosambiquensis* in Mozambique has long been an anomaly in accounts of the freshwater Mollusca of southern Africa (Connolly 1925; Pilsbry & Bequaert 1927; Connolly 1939; de Azevedo *et al*. 1961; Brown 1980, 1994). Six syntypes of *P. mosambiquensis* are lodged in the Berlin Museum under the accession number ZMB Moll. 8484 (Kilias 1961) and were kindly loaned by Dr M. Glaubrecht. One of the shells has Byne's disease and is therefore kept in a separate vial under the number 8484a. There are six handwritten labels in the Berlin Museum storage box containing the shells and these are shown in chronological order in Fig. 1. Three (Figs 1A–C) appear to have been written before Clessin's identification and two (Figs 1A, 1C) bear the number '8' which may indicate that there were originally eight shells.

No further finds of *P. mosambiquensis* were reported from Mozambique by Connolly (1925) or de Azevedo *et al*. (1961) but snails which conform to this species were discovered in Durban, South Africa, in 1986 (Appleton *et al*. 1989), exactly 100 years after Clessin's description. These snails, called *Aplexa marmorata* by Appleton *et al*. (1989) and Appleton (1996, 2002), are spreading in South Africa (Appleton 2003), especially in KwaZulu-Natal and Mpumalanga provinces, with a recent find at Ponta da Ouro in the extreme south of Mozambique, close to the KwaZulu-Natal border.

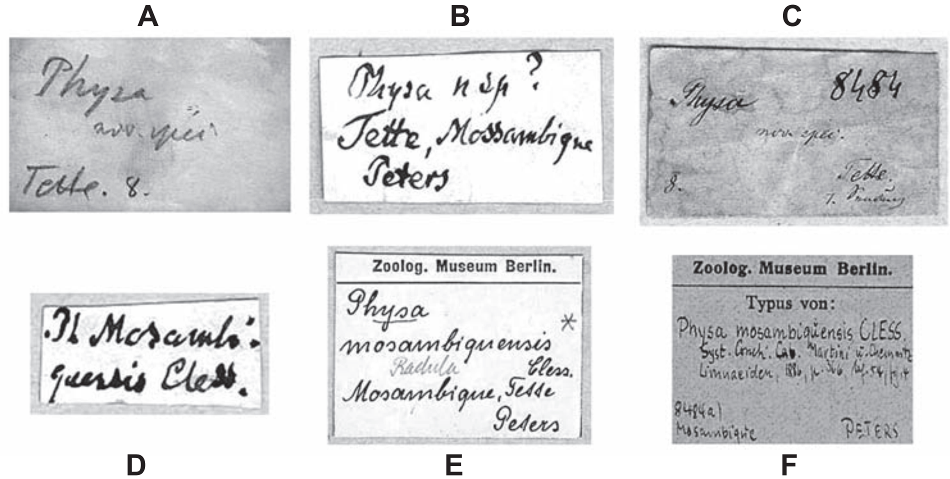

Fig. 1 A–F. Labels in the Berlin Museum box containing the six syntypes of *P. mosambiquensis* arranged in chronological order. With two exceptions (indicated by dotted lines), the handwriting is legible as follows (authors in brackets): (A) '*Physa* nov. spec., Tette. 8.', (?Peters); (B) '*Physa* n. sp.? Tette, Mossambique, Peters', on reverse '8484 ….' (von Martens); (C) '*Physa* nov. spec., Tette. 8. ….', accession number 8484 added later (? von Martens); (D) '*Ph. Mosambiquensis* Cless.', and on reverse 'Cless 54.4' (von Martens); (E) '*Physa mosambiquensis* Cless., Mosambique, Tette, Peters' (an asterisk and the word 'radula' have been added to this label in pencil) (unknown assistant); (F) '*Physa mosambiquensis* CLESS. Syst. Conch. Cab. Martini u Chemnitz, Limnaeiden, 1886, p. 366, Taf. 54, fig. 4. 8484a, Mosambique, PETERS' (Kilias).

A re-examination of *P. mosambiquensis* is therefore desirable in order to compare it with *A. marmorata* and to unravel information on its origin in southern Africa.

Clessin's 1886 description of the shells of *P. mosambiquensis* was translated from Latin by Connolly (1939) as follows:

> 'Shell narrow ovate, hardly rimate, smooth, glossy, transparent, corneous yellow. Spire short, fairly acute. Whorls 4, elongate, little convex, rapidly increasing, last $^2/_3$ to $^3/_4$ of total length; suture little impressed. Aperture narrow piriform, acuminate above, peristome thin, acute, ends not united, columella thin, little contorted.'

He added that the first two whorls were practically smooth, the remainder showing faint, straight growth striolae. The illustration accompanying Clessin's (1886) description of *P. mosambiquensis* is reproduced here (Fig. 2A). Note that it appears as fig. 4 in Clessin's plate 54 and not fig. 1 as stated in his text.

Earlier, Connolly (1925) had illustrated the shell of *P. mosambiquensis* using a drawing given to him by J. Thiele (*in litt.*) (Fig. 2B). Thiele had commented that the drawing was of the largest specimen of *P. mosambiquensis* in the Berlin Museum (probably no. 3 in Table 1), and that its radula was typically physid in form, i.e. a central tooth with lateral and marginal teeth arranged in oblique rows on either side. Connolly reproduced this drawing again in his monograph (1939, text-fig. 41) and apart from that accompanying Clessin's (1886) description, it remains the only published illustration of *P. mosambiquensis*.

Thiele's mention of the radula of *P. mosambiquensis* indicates that the specimens were collected alive and the word 'radula' has been pencilled on one of the labels in the box containing the specimens (see Fig. 1E). According to Dr Glaubrecht (*in litt.*) however, there are neither radula preparations nor soft parts belonging to this species in the museum's collection and only the shells remain. What appear to be the dried remains of soft parts can in fact be seen inside the aperture of one of the type shells as shown in Fig. 2D.

RE-EXAMINATION OF *PHYSA MOSAMBIQUENSIS*

A re-examination of the shells of *P. mosambiquensis*, and the illustrations by Clessin (1886) and Connolly (1925, 1939), shows that they vary in shape from what Connolly (1945) calls 'a peculiar shuttle form', i.e. ventral margin pointed (Figs 2A, 2C), to one in which the ventral margin is noticeably truncated (Figs 2B, 2D).

Such variation is not unusual in physids as illustrated by Hamilton-Attwell *et al.* (1970) for *Physa acuta*, and the 'shuttle' shape noted by Connolly is typical of the Neotropical species *Physa marmorata* Guilding, 1828, as illustrated by Paraense (1986).

The protoconchs of three of the six shells are slightly damaged, as is the outer lip of the basal whorl on one of these. All intact lengths and maximum widths were plotted, and assuming allometric growth, the lengths of the damaged shells were estimated from the resulting equations: $L = 1.3396W + 1.4675$ ($R^2 = 0.9919$, n = 5) and $L = 1.3029A - 0.0442$ ($R^2 = 0.9957$, n = 5). Shell measurements and ratios for all six shells are given in Table 1.

Paraense (1986, 1987) drew attention to the presence of a sutural belt (or band) in the shell of *P. marmorata*, i.e. the area bounded by the sutural and subsutural lines, and its microsculpture. He described the belt as a wider but shallower (than *Physa cubensis*) 'whitish band' in which the raised growth lines are packed together giving a coarsely striate appearance. Although not mentioned by Clessin (1886), the belt is clearly visible

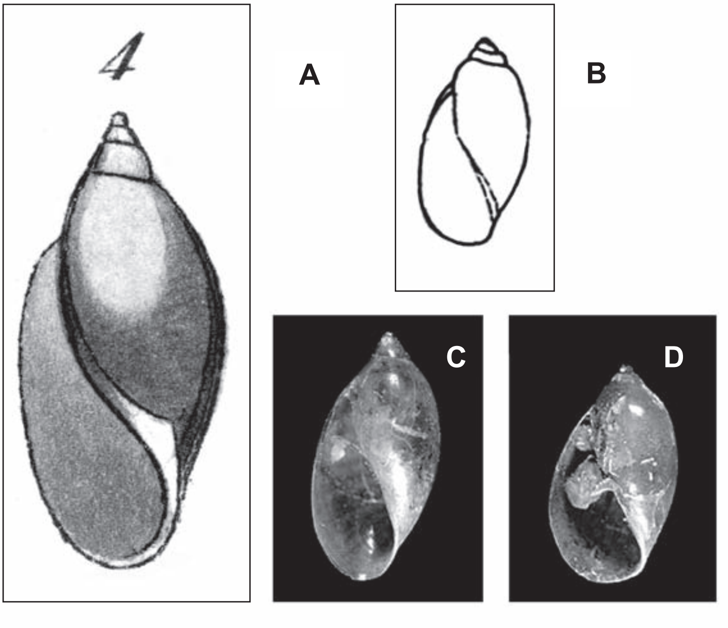

Fig. 2 A–D. *Physa mosambiquensis*: (A, B) published drawings: (A) fig. 4 (pl. 54) of Clessin (1886), (B) fig. 23 of Connolly (1925); (C, D) photographs of two syntypes: (C) 'shuttle-shaped' shell, (D) truncated shell.

TABLE 1

Measurements (L – length, W – maximum width, A – aperture, S – spire) and ratios (W/L, A/L, S/L) for six syntypes *P. mosambiquensis*. Measurements in brackets were estimated from the equations given above. * – protoconch damaged, ** – both protoconch and lip of basal whorl damaged. Specimen no. 1 has Byne's disease (cat. no. 8484a).

Specimen	L	W	A	S	W/L	A/L	S/L
1*	(6.36)	3.65	4.92	(1.45)	0.57	0.77	0.23
2	8.28	5.04	6.48	1.80	0.61	0.78	0.22
3*	(8.45)	5.21	6.40	(2.09)	0.62	0.76	0.25
4	5.82	3.20	4.47	1.35	0.55	0.77	0.23
5	6.89	4.14	5.37	1.52	0.60	0.78	0.22
6**	(6.69)	(3.90)	5.17	1.06	0.58	0.77	0.19
Mean SD	7.08 ±1.06	4.19 ±0.79	5.47 ±0.81	1.55 ±0.36	0.59 ±0.026	0.77 ±0.008	0.22 ±0.020

as a shallow, white band with a striate pattern of growth lines in all six syntypes of *P. mosambiquensis* and can be seen in Fig. 2C. It is hardly visible under the SEM (Fig. 3) because, as is evident when viewed under the light microscope, the belt lies inside the shell, presumably associated with one of its component layers. It is not a surface structure.

A sutural belt is also present on the shells of *A. marmorata* from Durban but not on those of *P. acuta*, the other invasive physid in Africa. Surprisingly Ranson and Cherbonnier (1951) did not refer to or illustrate any sutural belt on the shells of *P. waterloti* studied by them from Benin, noting only that the sutures were oblique and '*médiocrement marquées*'. This may have been an oversight since a belt is clearly visible on a shell from Ghana illustrated by Brown (1994).

The shells of *P. mosambiquensis* conform to the features used by Paraense (1987) to characterise *P. marmorata* from the Neotropical Region, i.e. flatly convex whorls, not shouldered; a high, narrow spire; shallow sutures and a low columellar plait. Ratios for shell dimensions (width/height, spire height/shell height, aperture height/shell height) vary considerably and provide no useful additional features. This variability may be an expression of the well-known plasticity of physid shells and of course, the small sample size of *P. mosambiquensis*. The shells ranged between 5.82–8.45 mm in height (mean 7.08 mm) (Table 1) and are thus small when compared to full-grown *marmorata* specimens from South Africa which reach 15 mm (Appleton 1996), from Brazil (approx. 16 mm) and from Peru where the largest collected shell was approx. 25 mm. (W.L. Paraense pers. comm.). Assuming that the shells of *P. mosambiquensis* were representative of the population sampled, the growth data given by Dana and Appleton (in press) for two Durban populations of *A. marmorata* suggests that they were between five and a half and seven and a half months old, a little over half-grown, and probably belonged to the same reproductively mature cohort.

TYPE LOCALITY OF *PHYSA MOSAMBIQUENSIS*

Appleton *et al*. (1989) discussed the interpretation of the locality information given for *P. mosambiquensis* by Connolly (1939). They were however unaware of a note on page 2 of that work, and in Connolly (1925), explaining that the use of '*Hab*. L. MARQUES' or '*Hab*. LORENZO MARQUES' indicated the whole area of southern

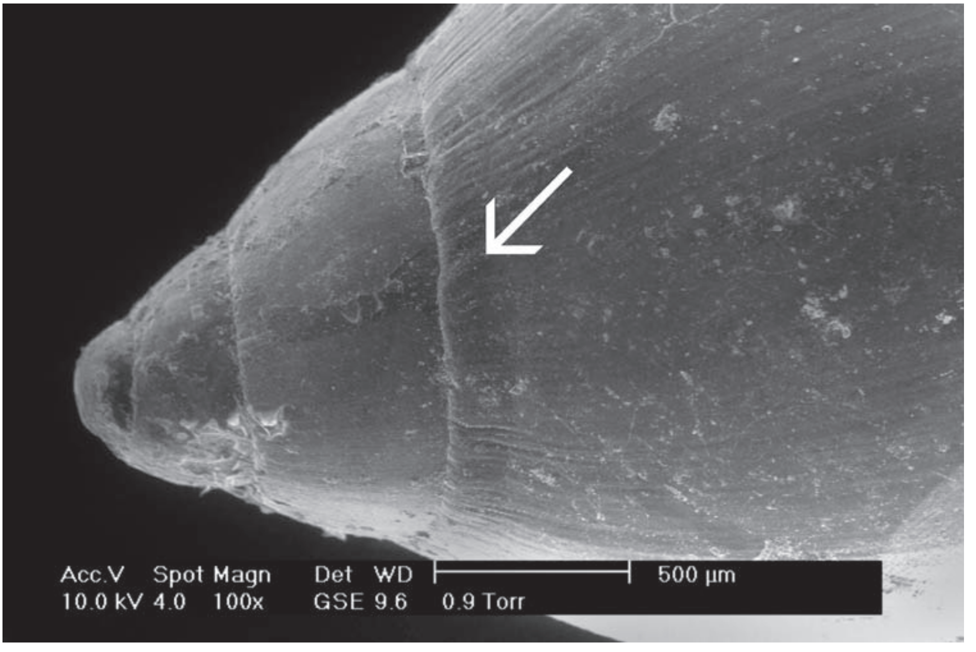

Fig. 3. ESEM micrograph of the spire of a syntype shell of *P. mosambiquensis* showing the sutural belt indicated by an arrow. Scale bar = 500 µm.

Mozambique south of the Zambezi River, and not just the city of Lourenço Marques (now Maputo). Connolly (1925) included a map of this area.

Tette (now Tete) in central Mozambique is generally cited as the type locality for *P. mosambiquensis*, and lies on the lower reaches of the Zambezi River at 16°10'S:33°35'E at an altitude of approximately 110 m. There is no reason to doubt that this is where *P. mosambiquensis* was collected even though Clessin in his 1886 description, gave only 'Mosambique' as the collection locality. The first authority to give Tete as the type locality was Connolly (1925), viz. '*Hab*. L. MARQUES. Tette (Peters)'. However, four of the six labels in the box containing *P. mosambiquensis* in the Berlin Museum have 'Tette' written on them (Fig. 1). Three of these, presumably the oldest labels, must have been written before Clessin's (1886) description since they refer to '*Physa* nov. spec.' and '*Physa* n. sp.' but not *Physa mosambiquensis* as the others do.

Unfortunately Clessin (1886) did not give any description of the habitat at Tete from which Peters collected *P. mosambiquensis*, not even whether it was natural or artificial. Assuming that other material would have been collected from the same waterbody(ies) as *P. mosambiquensis*, a search was made for locality data for other freshwater taxa collected by Peters at Tete. The list given by Von Martens (1879) of mollusc species collected by Peters in Mozambique does not mention *P. mosambiquensis*, since it was not described until 1886, though it does include eight other species (gastropods *Melanoides tuberculata*, *Lanistes ovum, L. purpureus, Bulinus africanus* and bivalves *Coelatura mossambicensis*, *Spathopsis wahlbergi, S. petersi*, *Corbicula fluminalis*) collected at Tete.

The locality data given for these specimens do not provide much insight as to the types of waterbody sampled by Peters, beyond indicating that they were predominantly riverine, associated with the Zambezi River. Although Peters' six-volume account of his expedition's collections (1852–1882) does not give any details on freshwater molluscs, a check of locality notes given for fish (Peters 1868) shows that he visited a number of rivers (*flumina*) and other waterbodies such as streams (*rivula*) and marshes (*paludes*) close to the coast between latitudes 15°S and 18°S. In the vicinity of Tete, however, he recorded only riverine collection sites, i.e. the Zambezi and Revugo rivers at or near Tete. There is thus no reason to suppose that *P. mosambiquensis* was collected at anything other than a riverine habitat. The inclusion of the vegetation-associated pulmonate *Bulinus africanus* in the list of species collected by Peters strongly suggests that marginal vegetation in slowly flowing or standing waters was sampled. Habitats of this type are known to support populations of *Aplexa marmorata* elsewhere (de Kock & Wolmarans 1998).

DISCUSSION

Relationship to other Physidae reported from Africa

A note by Connolly (1945) considered *P. mosambiquensis* to be conspecific with *P. waterloti* from West Africa. *P. waterloti* was described from Porto Novo in Dahomey (now Benin) by Germain (1911) but was placed in *Aplexa* by Brown (1994). Today it occurs in four contiguous countries on the coast of West Africa, viz. Ghana, Togo, Benin and Nigeria (Brown 1994). Details of the shell and anatomy of *P. waterloti* from Benin were provided by Ranson and Cherbonnier (1951).

The present study found that the shells of *P. mosambiquensis* were also indistinguishable from the shells of South African and Brazilian representatives of the species *marmorata*. This conclusion was supported by Dr W.L. Paraense (pers. comm.). It would be necessary to examine the soft parts to confirm this identification but, as noted above, they are no longer available. However, Te (1978) compared shells and anatomy of *P. waterloti* from Ghana and Nigeria with those of *marmorata* from the Caribbean and concluded that they belong to the same species. More recently, Appleton *et al*. (1989) and Dana (2000) compared the reproductive anatomy of members of the species *marmorata* from South Africa and St Lucia (Caribbean) and *waterloti* from Nigeria. These studies led to the conclusion that the African snails were indistinguishable from *marmorata* from South America and the Caribbean as re-described by Paraense (1986).

We conclude therefore that *P. mosambiquensis* from Mozambique, *P. waterloti* (*A. waterloti* following Brown 1980, 1994) from West Africa (Germain 1911; Ranson & Cherbonnier 1951) and *P. marmorata* from the Caribbean (Te 1978, as *Stenophysa*), Brazil (Paraense 1986) and South Africa (Appleton *et al*. 1989, as *Aplexa*) all represent the same species. In terms of precedence, Guilding's 1828 name *Physa marmorata* should apply, perhaps until the debate over the validity of the generic names *Aplexa* and *Stenophysa* has been settled. In line with this therefore, the species under discussion will be referred to the genus *Physa* for the remainder of this paper, with the following synonymy:

Physa marmorata Guilding, 1828

Physa marmorata Guilding, 1828: 534; Paraense 1986: 459–469, figs 1–33.
Stenophysa marmorata: Te 1978: 206, table 22; Taylor 2003: 113–121, figs 95–109.
Aplexa marmorata: Appleton *et al*. 1989.
Physa mosambiquensis Clessin, 1886: 366, pl. 54, fig. 4; Connolly 1925: 189, fig. 23; 1939: 475, text fig. 41; 1945: 167; Appleton *et al*. 1989 [considered a synonym of *marmorata*].
Physa waterloti Germain, 1911: 322, fig. 57; Connolly 1945: 167 [synonymised under *mosambiquensis*].
Aplexa waterloti: Brown 1980: 213, fig. 115; 1994: 249, 250, fig. 115.

This opinion is in agreement with that of Taylor's (2003) revision of the Physidae inasmuch as the material from both west and south-eastern Africa represents a single species that originated in South America, probably Brazil. Taylor considers, however, that the name *Afrophysa brasiliensis* given to the West African snails by Starobogatov (1967) should be retained and should also apply to the southern African material. From a detailed comparative study of male genital morphology, he argues that the species *marmorata* (as *Stenophysa*) is confined to the Caribbean islands (excluding Cuba) and a small area of the central American isthmus and that *A. brasiliensis* is native to the southernmost state of Brazil, Rio Grande do Sul. This latter distribution is incompatible with translocation to Africa aboard slave trade ships (see below) which would have sailed from more northerly ports such as Rio de Janeiro, Salvador (formerly Bahia) and Pernambuco. Relatively few slaves were taken to Argentina (W.L. Paraense pers. comm.).

Origin of Physa marmorata *in Africa*

It seems clear that Tete was the first collection site despite no mention of any precise type locality by Clessin (1886). This is important because it points to an early introduction of *P. marmorata* to south-eastern Africa. It seems likely that it was introduced from Brazil or the Caribbean islands via Portuguese sailing ships between the 16th and 19th centuries, possibly as a consequence of the slave trade. Most slaves taken to Brazil came from Angola but a substantial number came from Mozambique, as well as parts of East Africa (Magalhães & Dias 1944; de Lucena 1950; Harries 1981; Paraense 1997). In fact Harries (1981) noted that the slave trade between Mozambique, and Brazil and the Caribbean islands, flourished between about 1790 and the 1850s and that Quelimane, approximately 130 km north-east of the Zambezi River mouth, was '… the foremost slave embarkation point on the Mozambican coast'. It is possible therefore that *P. marmorata* was introduced to Mozambique during the height of the slave trade, i.e. during the decades immediately preceding its discovery at Tete by Peters.

A question raised by D.W. Taylor (*in litt*. to D.S. Brown, 13.1.1988) is relevant here, viz. why was the only known locality for *P. mosambiquensis* situated inland at Tete and not on the coast? He speculated that the specimens may have represented the spread inland from an inoculum on the coast. The answer may lie in the fact that, as the enforcement of the prohibition of slavery began to take effect in the late 1830s, slavers avoided recognised ports and instead used hidden embarkation points such as river mouths. Dr Livingstone demonstrated with the *Ma Robert* in 1858, that the Zambezi River was navigable for small steamers as far as the rapids at Tete, approximately 410 km from the coast. An intriguing twist to this practice was a claim by Livingstone, quoted in a footnote in the foreword to Volume IV of Peters (1852–1882) accusing the Portuguese authorities in Mozambique of deliberately producing maps which showed the mouth of the Zambezi as the Kwakwa River at Quelimane, nearly 100 km north of its true position. This error was perpetuated in maps issued later by the Colonial Minister of Portugal and was, so Livingstone believed, designed to induce British ships enforcing the ban on slave trafficking, to station themselves well north of the real embarkation point. Whatever the case, slave trading from secluded embarkation points in defiance of the ban would have given traders direct access to natural fresh waters and, in the case of the Zambezi, to villages well inland.

Long-distance translocation of freshwater invertebrates aboard sailing ships is not far-fetched. The mosquito *Aedes aegypti*, vector of yellow fever, is believed to have been transported from West Africa to South America and the Caribbean islands in water barrels on slaving ships in the early 1600s (Spielman & D'Antonio 2001). Dumont & Martens (1996) suggest that the cladoceran *Alona weinecki* and an ostracod *Sarscypridopsis* sp., both sub-Antarctic species, were introduced to Easter Island by human agency. Indeed, the appearance of *A. weinecki* in cores from the lake in Rano Raraku crater coincides with Captain Cooke's visit to the island in 1774 (H. Dumont pers. comm.).

In view of the distance of over 1500 km between the recent finds in South Africa and the 1886 record of *P. mosambiquensis* in Mozambique (at Tete), it is tempting to relate these two records, and to propose that the species has been in south-eastern Africa for as long as 200 years. Although the species was not recorded by malacologists working in Mozambique during the 1950s and 1960s (de Azevedo *et al.* 1961), its recorded occurrence in the lowlands of eastern South Africa since 1986 indicates its spread in a broader region. Opinion of two former researchers at the Siegfried Annecke Institute in Tzaneen (Limpopo Province) was that the Tzaneen population (see Appleton *et al.* 1989) had been translocated there from somewhere in south-eastern Rhodesia (now Zimbabwe) by an official of the Union of South Africa Health Department working at the Institute. If true, this suggests an unusually long lag period and an exceptional example of the 'long fuse big bang' scenario thought to be common among invasive organisms (Williamson 2000). Bearing in mind Germain's (1911) comment that *P. waterloti* seemed to be a recent introduction to West Africa and suggestions by other authors (e.g. Te 1978) that it was probably introduced from the Caribbean via the slave trade, there might have been a lag period before the species was actually found in West Africa as well.

During the 18 years since its appearance in Durban, *P. marmorata* has spread widely over the city's metropolitan area and into the eastern lowlands of South Africa, particularly in the northern half of KwaZulu-Natal (see below). A second record for Mozambique, a wetland at Ponta da Ouro in the extreme south of the country, just north of the border with KwaZulu-Natal, was made by P.E. Reavell in May 2004 but this is probably an extension of its northwards spread through KwaZulu-Natal.

This picture is however complicated by an enigmatic record by Brand *et al.* (1967) of *P. mosambiquensis* from the low gradient Valley Sand Bed Zone (head of estuary to 233 m altitude) of the Umgeni River, Durban. The collections on which Brand *et al.*'s survey was based were made between 1958 and 1962 by the National Institute for Water Research, Durban, but the location of the material is not known and the identification cannot be checked. Although this record may have been based on elongate specimens of *P. acuta* (it coincides with the first report of *P. acuta* in South Africa, viz. Umsinduzi River, Pietermaritzburg, 1958), the Umgeni River runs close to Pinetown where *P. marmorata* was discovered in 1986, about 25 years later. *P. marmorata* may therefore have been introduced into South Africa in the 1950s but did not become invasive until the 1990s.

Strangely *P. mosambiquensis* was not recorded by Schoonbee (1964) in his account of the 1958–1962 Umgeni River survey which also formed the basis for Brand *et al*.'s later 1967 report. More mollusc species were however recorded from the Valley Sand Bed Zone of the Umgeni by Brand *et al*. (1967) than by Schoonbee (1964) and this

TABLE 2

List of the 29 localities for *P. marmorata* in south-eastern Africa as shown in Fig. 4, with latitude, longitude and altitude for each locality.

Locality no. on map	Locality	Latitude, S	Longitude, E	Altitude (m)
1	pool near Hibberdene	30.5860	30.5547	89
2	lake, Bluff Nature Reserve	29.9373	30.9936	1
3	dam, Kenneth Stainbank Nature Reserve	29.9111	30.9333	163
4	canal, Newlands	29.8000	30.9500	5
5	pond, Pinetown	29.8000	30.8833	359
6	ponds, Durban Botanic Gardens	29.8480	31.0068	20
7	Beachwood pond	29.7903	31.0466	1
8	Durban North sewage works	29.7077	31.0820	113
9	pond in Phoenix	29.6980	31.0223	158
10	Amatikulu Fish Farm	29.1250	31.6250	2
11	weir on Siyaya River, Mtunzini	28.9811	31.7355	45
12	wetland along N2 between Mtunzini and Empangeni	28.8500	31.4333	587
13	Richards Bay	28.7731	31.9806	34
14	Richards Bay	28.7756	32.0056	30
15	stream outside Empangeni	28.7174	31.8776	93
16	wetland on road from Lake Nhlabane to Mapelane	28.4824	32.2822	11
17	pan on western shore of Lake St Lucia	28.0833	32.4333	10
18	Suni Ridge Game Farm, Hluhluwe	28.0167	31.9833	458
19	wetland, Ponta da Ouro, South Africa/ Mozambique border	26.8531	32.8856	1
20	Mlambanespruit, Kruger National Park	25.3572	31.5197	303
21	Matjuluspruit, Kruger National Park	25.3572	31.5197	303
22	Gezantombi Dam, Kruger National Park	25.3347	31.8764	144
23	Mbyamiti River, Kruger National Park	25.2242	31.5772	278
24	Vervoer Dam, Kruger National Park	25.1186	31.4914	416
25	Sabie River, Kruger National Park	25.1183	31.9167	157
26	Sunset Dam, Kruger National Park	25.1158	31.9114	145
27	Mestel Dam, Kruger National Park	25.1150	31.2139	575
28	artificial pond, Tzaneen	23.8333	30.1667	726
29	Tete, Mozambique (no habitat data)	16.1667	33.5833	110

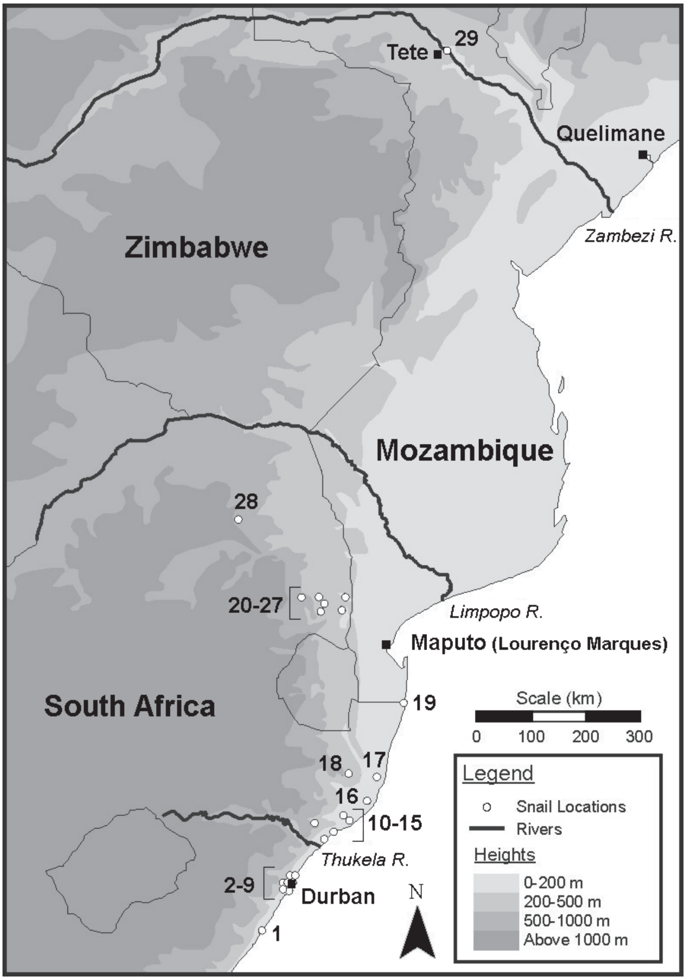

Fig. 4. Map of south-eastern Africa showing Tete, Mozambique, where syntypes of *P. mosambiquensis* were collected by Peters in the 1840s (Connolly 1925, 1939), relative to the localities where *P. marmorata* has been collected since 1986. Most localities are contained within the 200 m altitudinal contour.

appears to be due to more careful identification by Brand *et al*. Schoonbee may not have recognised the physid since this family was at that time virtually unknown in South Africa.

Distribution of Physa marmorata *in South Africa*

P. marmorata is spreading in South Africa and has become the third most widespread invasive freshwater snail in the country after *Lymnaea columella* and *P. acuta* (Appleton & Brackenbury 1998; Appleton 2003). Since its discovery in the Durban area in 1986 it has been collected from 29 localities in the low-lying parts of three eastern provinces, mostly in KwaZulu-Natal and Mpumalanga, with an isolated record in Limpopo (Table 2, Fig. 4).

These localities all lie below an altitude of 726 m, with 26 (89%) below 500 m and 20 (69%) below 200 m on the coastal plain. They include many types of lentic waterbodies, both natural (e.g. streams, small lake, pools and pans) and artificial (e.g. dams, canals and concrete-lined ponds). Exceptions are the records from a backwater in the perennial Sabie River and three seasonal streams in the Kruger National Park, Mpumalanga (de Kock & Wolmarans 1998; de Kock *et al*. 2002). Notes on these watercourses (K.N. de Kock pers. comm.) describe low snail densities in clear, slowly flowing water with substrata of sand, stone and decaying organic matter and generally sparse emergent and/or floating vegetation.

Since habitats in most localities (Fig. 4) are lentic or slowly flowing, it seems that, compared to the related *P. acuta*, *P. marmorata* is less able to colonise large flowing watercourses. This may explain its virtual absence from the country's major river systems, a factor that could be slowing its spread. However, the aggregation of localities (numbers 20–27) in the southern part of the Kruger National Park, an area where dispersal by human agency can probably be discounted, suggests that similarly comprehensive surveys in other areas would show a wider geographic distribution. The study by de Kock *et al*. (2002) ascribed the species' spread in this area between 1995 and 2001 to passive transport via floods during a period of abnormally high rainfall. Annual rainfall figures measured during this period at five stations in the newly colonised area ranged from 39 to 95% (mean 69%) higher than the mean of the previous five years (466 mm).

Interspecific differences in habitat preference were also observed by the senior author in rivers, streams and irrigation furrows in several districts of Rio de Janeiro State, Brazil, in August 2000. *Physa cubensis*—equated with *P. acuta* by Paraense and Pointier (2003)—was the only physid present (often abundant) in larger, flowing rivers, while both it and *P. marmorata* occurred (though only in moderate numbers) in smaller channels where flow was generally slight or lacking.

A similar situation was observed in Puerto Rico, where Harry and Hubendick (1964) noted that *P. marmorata* and *P. cubensis* had different habitat preferences. They reported that '*P. cubensis* occurs in the larger streams of low gradient, but *P. marmorata* does not seem to occur there. *P. cubensis* extends into the steeper gradient headwater streams where the individuals are small and rare, but *P. marmorata* was not found in such habitats'.

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