

The use of screw pines (*Pandanus* spp.) by amphibians and reptiles in Madagascar

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ABSTRACT. — The importance of plant-held water bodies (phytotelmata) to amphibians and reptiles has been recognised in many tropical environments. However, water-holding plants from Madagascar have not been investigated in this regard. I surveyed screw pine (*Pandanus*) plants at two localities in southeastern Madagascar to document usage of these micro-aquatic habitats by amphibians and reptiles. Twenty species (nine frogs, six geckoes, four snakes, and one skink) were found in these plants (32% of the total estimated herpetofauna of the area). At least five species are obligate *Pandanus*-dwellers, while others facultatively used the water-filled leaf axils of these plants. A literature review indicates that at least twenty-one additional species in Madagascar are commonly or exclusively found in *Pandanus* plants. This information demonstrates the importance of these unique microhabitats to Madagascar's poorly known and highly endemic herpetofauna.

BROMELIADS in the neotropics provide a unique aquatic microhabitat for numerous species of amphibians and reptiles (e.g., Dunn 1937). Some species are specialised bromeliad breeders and are completely dependent on these aquatic environments to complete their lifecycle (Lannoo et al., 1987). Plants from the paleotropics in the genus *Pandanus* (Pandanaeae, 'screw pines') are analogous to bromeliads in many respects. Like bromeliads, many screw pines hold rainwater in their leaf axils (i.e., they are phytotelms) and these micro-aquatic environments are used by a wide assortment of animals, including some reptiles and amphibians (Fish, 1983).

Screw pines are widespread in the paleotropics (approximately 600 *Pandanus* species total, 85 in Madagascar; Schatz 2001) and can be found in many environments. Those *Pandanus* that retain rainwater in their leaf axils can provide an important habitat for reptiles and, especially, amphibians. While Wassersug et al. (1981) stated that tree holes and tree buttresses were the primary phytotelm habitats in tropical Asian forests, several species of anurans are known to breed in water-filled *Pandanus* leaf axils (e.g., *Pelophryne brevipes*, *Philautus lissobranchius*, Alcalá & Brown 1982; *Platymantis vitiensis*, Gibbons & Guinea 1983).

In Madagascar, *Pandanus* plants are utilised by amphibians and reptiles for a variety of activities such as breeding, resting and feeding. Some specialised species are obligate *Pandanus*-dwellers and rely exclusively on these plants throughout their life cycle. However, despite the importance of these microhabitats, there has been no attempt to summarise the available information on the herpetofauna of *Pandanus*. My objective here is to summarise and describe the herpetofauna of *Pandanus* from two localities in southeastern Madagascar, and briefly discuss what is known from the rest of the island from data available in the literature.

MATERIALS AND METHODS

I surveyed six fragments of coastal rainforest at two sites in the Fort-Dauphin (Tolagnaro) region of southeastern Madagascar (Mandena 24°57'S; 47°02'E; Sainte Luce 24°46'S; 47°10'E) for amphibians and reptiles. These surveys were conducted as part of a detailed study of the population ecology of *Pandanus*-dwelling frogs in this area (the details of which will be published elsewhere). *Pandanus* plants were sampled visually by inspecting all leaf axils for the presence of amphibians or reptiles. *Pandanus* that had their crowns more than 2 m but less than 4 m

above the forest floor were sampled using a step ladder 1.5 m high. *Pandanus* greater than 4 m in height were sampled by ascending adjacent trees using tree climbing equipment (Laman, 1995). *Pandanus* sampling occurred during the day and at night with the aid of a headlamp. Combined, over 1700 individual *Pandanus* plants of all sizes were sampled. Each plant was searched from one to nine times over the study period for a total of over 8400 observations. Other habitats in this area (e.g., leaf litter, woody debris, sand-scrub, streams, ponds) were also formally surveyed for amphibians and reptiles during this and previous survey efforts using transects, pitfall traps and opportunistic searching (Ramanamanjato, 2000).

Presence-absence data were compiled from all *Pandanus* observations from Mandena and Sainte Luce (1999 - 2002). Frequency data were obtained from permanent plots at Sainte Luce (2000 - 2002). Facultative and obligate *Pandanus*-dwelling species were differentiated based on survey results from *Pandanus* and non-*Pandanus* habitats. Species found only in *Pandanus* were categorised as obligate, those also found elsewhere were categorised as facultative. Surveys were conducted in 1999 (31st May to 21st June - dry season), 2000 (3rd February to 28th March - wet season) 2001 (14th January to 26th February) and 2002 (24th January to 3rd March). See Ramanamanjato (2000) for more information on the study area.

Reference specimens of all amphibians and reptiles found in *Pandanus* were deposited at the University of Michigan Museum of Zoology and the Département de Biologie Animale at the Université d'Antananarivo, Madagascar. Other records of amphibians and reptiles in *Pandanus* from Madagascar were collected from the literature and from the observations of other researchers.



Figure 1 (above). Adult *Mantidactylus bicalcaratus* on *Pandanus* leaf, Sainte Luce, Madagascar. © Richard Lehtinen.

Figure 2 (below). Adult female *Phelsuma quadriocellata* immediately after depositing two eggs in a *Pandanus* leaf axil, Sainte Luce, Madagascar. Colour returned to normal within 30 s. © Richard Lehtinen.

RESULTS

Twenty species of amphibians and reptiles were detected in *Pandanus* at Sainte Luce and Mandena (nine frogs, six geckoes, four snakes, and one skink; Table 1). Five of these species were deemed obligate *Pandanus*-dwellers, including three frogs in the genus *Mantidactylus* that complete their entire life cycle in *Pandanus* plants (Fig. 1). The remaining *Pandanus*-obligate species are two

Species	Reproduction in <i>Pandanus</i>	<i>Pandanus</i> Use	Life Stage	Season	Height (m)	Frequency (%)
<i>Boophis madagascariensis</i>	N	Facultative	Adults	Wet season	near ground	< 1
<i>Mantidactylus bicalcaratus</i>	Y	Obligate	All	Year round	7 m	48.1
<i>Mantidactylus boulengeri</i>	N	Facultative	Adults	Year round	near ground	< 1
<i>Mantidactylus depressiceps</i>	N	Facultative	Juveniles, Adults	Dry season	4 m	1.3
<i>Mantidactylus cf. pulcher</i>	Y	Obligate	All	Year round	5 m	1.7
<i>Mantidactylus punctatus</i>	Y	Obligate	All	Year round	11 m	14.4
<i>Mantidactylus cf. wittei</i>	N	Facultative	Adults	Year round	near ground	< 1
<i>Plethodontohyla notosticta</i>	N	Facultative	Adults	Year round	near ground	< 1
<i>Heterixalus boettgeri</i>	N	Facultative	Adults	Dry season	near ground	< 1
<i>Boa manditra*</i>	N	Facultative	Adults	Year round	3 m	< 1
<i>Ithyocyphus oursi</i>	unknown	Facultative	Adults	Year round	5 m	< 1
<i>Liopholidophis cf. stumpffi</i>	N	Facultative	Adults	Wet Season	near ground	< 1
<i>Madagascarophis colubrinus</i>	N	Facultative	Adults	Year round	near ground	< 1
<i>Ebenavia inunguis</i>	unknown	Facultative	Juveniles, Adults	Wet Season	near ground	2.5
<i>Geckolepis maculata</i>	Y	Facultative?	Adults	Year round	7 m	< 1
<i>Hemidactylus mercatorius</i>	N	Facultative	Adults	Dry Season	unknown	< 1
<i>Phelsuma antanosy</i>	Y	Obligate	All	Year round	2 m	NA
<i>Phelsuma quadriocellata</i>	Y	Obligate	All	Year round	3 m	10.9
<i>Phelsuma lineata</i>	unknown	Facultative	All	Year round	3 m	< 1
<i>Amphiglossus punctatus</i>	unknown	Facultative?	Juveniles, Adults	Year round	5 m	< 1

Table 1. Data on amphibians and reptiles found in *Pandanus* at Sainte Luce and Mandena, southeastern Madagascar, 1999-2002. Height (m) is the maximum height at which each species has been found in *Pandanus*. Frequency is the proportion of *Pandanus* occupied by each species in 2001 (unavailable for *P. antanosy* - not present in permanent plots).

* = *Sanzinia madagascariensis*.

geckos in the genus *Phelsuma* (Fig. 2). The remaining species from Sainte Luce and Mandena appear to inhabit *Pandanus* plants facultatively.

Amphibians and reptiles were found in three different species of screw pines (*Pandanus platyphyllus* and two undescribed species). *Mantidactylus cf. wittei* was found only in *P. platyphyllus* (usually at the forest edge or in deforested areas). *Boophis madagascariensis* was found on two occasions on an undescribed stream species of *Pandanus*. *Phelsuma lineata* and *P. quadriocellata* were also found several times on this stream species. All other records of amphibians and reptiles in this study were from an

undescribed species of phytotelmic, terrestrial *Pandanus* (M. Callmander, pers. comm.).

Several species occurred in a relatively high proportion of *Pandanus* in the permanent plots. *Mantidactylus bicalcaratus* (48.1%), *M. punctatus* (14.4%) and *Phelsuma quadriocellata* (10.9%) were the most common. All other species were found in three percent or less of the *Pandanus* in the permanent plots (Table 1). Most species found in *Pandanus* were found only in those plants on or near the forest floor. Several species, however, were found in *Pandanus* as high as 11 m in the canopy. Some species were found in *Pandanus* only in the dry season or wet season, but most were found in *Pandanus* year round (Table 1).

A literature review revealed 21 additional species that are frequently or exclusively found in association with *Pandanus* in Madagascar (Table 2). These include 16 frogs, four geckos and a snake. Several of these also appear to be obligate *Pandanus*-dwellers.

Family	Species	Reproduction in <i>Pandanus</i>	<i>Pandanus</i> Use	Data Source	
Colubridae	<i>Lycodryas</i> (= <i>Stenophis</i>) <i>gaimardi</i>	unknown	Facultative	R. Nussbaum, pers. comm.	
Gekkonidae	<i>Paroedura bastardi</i>	N	Facultative	R. Nussbaum, pers. comm.	
	<i>Phelsuma dubia</i>	unknown	unknown	Glaw & Vences, 1994	
	<i>Phelsuma guttata</i>	unknown	unknown	Raxworthy, 1988	
Hyperoliidae	<i>Heterixalus alboguttatus</i>	N	Facultative	Blommers-Schlösser, 1982	
	<i>Heterixalus tricolor</i>	N	Facultative	Razarihelisoa, 1974	
Mantellidae	<i>Boophis apisthodon</i>	N	Facultative	C. Raxworthy, pers. comm.	
	<i>Boophis tephraeomystax</i>	N	Facultative	C. Raxworthy, pers. comm.	
	<i>Mantella laevigata</i>	N	Facultative	H. Heying, pers. comm.	
	<i>Mantidactylus albolineatus</i>	Y	Obligate	Blommers-Schlösser, 1979	
	<i>Mantidactylus flavobrunneus</i>	Y	Obligate	Blommers-Schlösser, 1979	
	<i>Mantidactylus liber</i>	N	Facultative	Blommers-Schlösser, 1979	
	<i>Mantidactylus peraccae</i>	N	Facultative	Blommers-Schlösser, 1979	
	<i>Mantidactylus tornieri</i>	N	Facultative	Blommers-Schlösser, 1979	
	<i>Mantidactylus webbi</i>	N	Facultative	H. Heying, pers. comm.	
	Microhylidae	<i>Anodonthyla boulengeri</i>	N	Facultative	H. Heying, pers. comm.
		<i>Anodonthyla rouxae</i>	Y	Obligate?	Glaw & Vences, 1994
<i>Platypelis barbouri</i>		unknown	unknown	Blommers-Schlösser, 1975	
<i>Platypelis grandis</i>		unknown	Facultative	R. Nussbaum, pers. comm.	
<i>Platypelis tuberifera</i>		Y	Obligate	Blommers-Schlösser, 1975	
<i>Plethodontohyla inguinalis</i>		N	Facultative	Andreone & Randriamahazo, 1997	

DISCUSSION

A relatively large proportion of the herpetofauna in the study area use *Pandanus* plants for a variety of activities (32% - 20 of an estimated 62 forest species; Ramanamanjato, 2000). Some species are obligate *Pandanus*-dwellers, such as the mantellid frogs *Mantidactylus bicalcaratus*, *M. cf. pulcher* and *M. punctatus*. These frogs lay egg masses on the leaves of phytotelmic *Pandanus* (not in tree holes as reported in Lannoo et al., 1987). After 3-12 d the jelly dissolves and the hatchlings wriggle down the leaf into the water-filled leaf axil to continue their larval development (R. Lehtinen, unpublished data). Unlike many phytotelmic anurans, however, these species also remain exclusively on *Pandanus* plants as juveniles and adults. Twenty or more individuals of these species can be found in large *Pandanus* and all three species can be found in a single plant. Other frogs are also frequently found in *Pandanus*, but are not dependent on these plants to complete their life cycle (Table 1).

Table 2. Other records of amphibians and reptiles from *Pandanus* in Madagascar.

It is not particularly surprising that screw pines are important habitats for frogs in Madagascar. Frogs have been reported from *Pandanus* in the Philippines (Alcala & Brown, 1982; Das & Charles, 1994), New Guinea (Allsion & Kraus, 2000), Fiji (Gibbons & Guinea, 1983), and other localities in the paleotropics. Reptiles, however, have less frequently been reported from *Pandanus*. My observations indicate that screw pines are also important microhabitats for some snakes, skinks, and geckos.

Several geckos use *Pandanus* plants for reproductive activities. The recently discovered day gecko *Phelsuma antanosy* is almost invariably associated with *Pandanus* plants and lays its eggs only in *Pandanus* leaf axils (Raxworthy & Nussbaum, 1993a; J.-B. Ramanamanjato, pers. comm.). This regional endemic is only known from four unprotected sites, one of which has

recently been destroyed (Raxworthy & Nussbaum, 2000). *Phelsuma quadriocellata*, also lays eggs in *Pandanus* leaf axils (Fig. 2). In this species, a single male and female, and sometimes one or more juveniles or egg clutches, are often found on suitable *Pandanus*. Individuals forage widely and are often found on adjacent vegetation (R. Lehtinen, unpublished data). *Phelsuma lineata* was also frequently found on *Pandanus* plants and may reproduce there, but this species also lays its eggs in other habitats. A fish-scale gecko, *Geckolepis maculata*, is frequently found in large *Pandanus* plants and eggs of this species have been found there (R. Nussbaum, pers. comm.).

Other reptiles are more facultative inhabitants of screw pines. The nocturnal snakes *Boa manditra* and *Madagascarophis colubrinus* are often found resting in *Pandanus* during the day, usually in the leaf axils or, less commonly, coiled around the trunk at the base of the plant. *Ithycyphus oursi*, by contrast, is diurnal and frequents *Pandanus* plants to hunt for frogs. At Sainte Luce, I witnessed *I. oursi* hunt and consume adult *Mantidactylus bicalcaratus*, *M. depressiceps* and *M. punctatus*. Geckos may also frequent *Pandanus* plants for feeding, as insects congregate to breed in the water-filled leaf axils. The recently described skink *Amphiglossus punctatus* is an interesting case, as it is found both on the forest floor and in aerial *Pandanus* (up to 5 m high) at Sainte Luce. All other known members of this genus are primarily fossorial or semi-aquatic (Raxworthy & Nussbaum 1993b).

Obligate *Pandanus*-dwelling species are, predictably, found on *Pandanus* year round. Of those species that use *Pandanus* facultatively, most are also found in *Pandanus* year round. However, several species are only found in *Pandanus* during the dry season (*H. boettgeri*, *M. depressiceps*). During the rainy season these species breed in lentic water bodies in (*M. depressiceps*) and out (*H. boettgeri*) of forest (R. Lehtinen, unpublished data). Dry season *Pandanus* use by these species is likely the result of relatively cool, moist conditions in *Pandanus* leaf axils. This suggests these species may use *Pandanus* primarily for thermoregulatory and

water balance functions in the dry season.

Not surprisingly, most species that were deemed obligate *Pandanus*-dwellers are found in a relatively high proportion of the plants sampled and most facultative *Pandanus*-dwellers were found in a relatively low proportion. However, some species, such as *Mantidactylus cf. pulcher* and *Ebenavia inunguis* do not fit this pattern well. (Table 1). This may be due to sampling error or to an incomplete knowledge of the natural history of these species. For example, future research may discover that *Ebenavia inunguis* lays eggs in *Pandanus*. Other phytotelmic plants (particularly *Ravenala madagascariensis* (Strelitziaceae) and *Typhonodorum lindleyanum* (Araceae)) are also sometimes used by amphibians and reptiles in Madagascar but are rare in this particular area.

These data indicate that *Pandanus* are important microhabitats for many species of amphibians and reptiles in Madagascar. This simple fact has not previously been appreciated and these key environments clearly are deserving of further study. In addition to my field data, a literature review indicates that numerous other amphibians and reptiles (particularly frogs and geckos; Table 2) in Madagascar also use *Pandanus*. This list is undoubtedly incomplete and future research will likely reveal many other species that use these micro-aquatic habitats. However, these plants have become rare in some areas. The leaves of *Pandanus* plants are used by villagers to weave baskets, hats, and other products and harvesting these leaves is often done by cutting down the entire plant. Also, *Pandanus* are slow growing and appear to germinate poorly in degraded conditions (R. Lehtinen, unpublished data). While forests in general are in dire need of protection in Madagascar, *Pandanus* plants may merit particular attention as they provide a key resource to many species.

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