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TREE-CLIMBING CRABS (POTAMONAUTIDAE AND SESARMIDAE) FROM PHYTOTELMIC MICROHABITATS IN RAINFOREST CANOPY IN MADAGASCAR

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ABSTRACT

The ecology of two species of tree-climbing crabs, *Malagasya antongilensis* (Rathbun, 1905) (Potamonautidae) and *Labuanium gracilipes* (H. Milne Edwards, 1853) (Sesarmidae), collected from container microhabitats (phytotelmata) in rainforest in the Masoala Peninsula, Madagascar, is described. This is a rare report of a tree-climbing phytotelmic sesarmid crab living in the rainforest canopy, and the first record of a species of true freshwater crab in the canopy, albeit at a relatively low height. The difficult-to-access rainforest canopy surveys were made as part of the Canopy Raft Program (Radeau des Cimes). The occurrence of crabs in water-filled plant containers in rainforest habitats is discussed.

We report here on the interesting discovery of two species of tree-climbing crabs belonging to two families (Potamonautidae and Sesarmidae) that were collected from container microhabitats (phytotelmata) in rainforest in the Masoala Peninsula on the northeast coast of Madagascar. This isolated peninsula supports one of the last undisturbed intact primary humid tropical forests in Madagascar, and is free from much of the human encroachment that has caused the environmental problems seen elsewhere on that island (Bradt *et al*., 1996).

Most faunal surveys of rainforest ecosystems have necessarily focused on areas that are accessible from the ground, but the present study, as part of the Canopy Raft Program (CRP, Radeau des Cimes, http://www.Radeau-des-Cimes.org), has surveyed all levels of the forest, including the canopy. Special attention was paid here to phytotelmata because crabs (as well as other arthropods and frogs) often exploit water pools in leaf axils, tree holes, and crevices within branches because these provide moist humid conditions both within the rainforest understory, and in the high canopy layers exposed to drying winds (Dunn, 1937; Maguire, 1971; Fitzjarrald and Moore, 1987; Lim and Ng, 1991; Denzer, 1994; Kitching, 2000, 2001).

Tree-living phytotelmic sesarmids include *Metopaulias* Rathbun, 1918, from tropical America (Hartnoll, 1964; Von Hagen, 1977; Diesel, 1989, 1991; Abele, 1992; Diesel and Schuh, 1993; Diesel and Schubart, 2000) and other sesarmids such as species of *Geosesarma* De Man, 1892 (see Thienemann, 1934; Ng, 1988, 1995), *Labuanium* Serène and Soh, 1970 (see Ng and Liu, 2003), and *Scandarma* Schubart, Liu, and Cuesta, 2003 (see Schubart *et al*., 2003) from the Indo-West Pacific. Not all tree-climbing sesarmids are phytotelmic, and there are a number of species that lay their eggs directly into the sea, and climb trees for protection, concealment, and a source of fresh leaves to eat, rather than as a provider of a freshwater microhabitat for their larval stages. For example, species of tree-climbing sesarmid crabs that are not known to be phytotelmic have been reported from Tanzania (Hartnoll, 1975), Kenya (Vannini and Ruwa, 1994; Vannini *et al*., 1997), Singapore (Sivasothi, 2003), and Taiwan (Jeng *et al*., 2003; Schubart *et al*., 2003).

In addition to sesarmids, a growing number of species of true freshwater crabs are recognized to inhabit container habitats in rainforest ecosystems in Africa (Cumberlidge, 1991, 1996a, b, 1999; Cumberlidge and Sachs, 1991, 2000; Bayliss, 2002; Cumberlidge and Vannini, 2004) and in mangrove ecosystems in Asia (Ng, 1991a, 1995). The present report of two little-known species of tree-climbing crabs living in container microhabitats at different levels of the rainforest canopy in Madagascar represents the first record of this nature for the island, and constitutes new distribution records for these two species.

MATERIALS AND METHODS

This study took place in the Masoala National Park (MNP) on the west coast of the Masoala peninsula in northeast Madagascar (Fig. 1), which is one of the wettest places on the island with an annual rainfall of over 350 cm per year. The MNP comprises 2100 sq. km of land plus three marine reserves, and includes the largest piece of primary lowland tropical forest in Madagascar (Kremen *et al*., 1999). The specimens reported on here were collected as part of the Canopy Raft Program (Radeau des Cimes) that provided a basecamp in the canopy and survey equipment to sample the forest in detail at all levels, from the forest floor to the canopy (Hallé, 1990). The survey equipment consisted of the canopy raft (Fig. 1C), a sled dragged underneath a dirigible (blimp), a bouyant balloon tied to a rope through the canopy, and two small, icosohedral "tree-houses," or Icos units (Icos I and II) set in canopy trees (Fig. 1A, B). Canopy searches were performed from the canopy raft, from the sled hung below the dirigible, from visual surveys from each of the two Icos units, and from canopy ascents using free ropes secured to trees. Other levels of the forest were sampled using pitfall trap arrays and opportunistic searching along forest trails during the day and night.

Between 24 October and 6 November 2001, four main sites on the Masoala Peninsula northeast of the base camp in Tampolo (Fig. 1D) were surveyed: east of Andranobe (Fig. 1A), east of Ambodiforaha (Fig. 1B), and along the coast between the two villages of Andranobe and Ambodiforaha (Fig. 1). The study area consisted of primary lowland and montane forests with relatively low canopy heights of 20 m, and emergent trees reaching

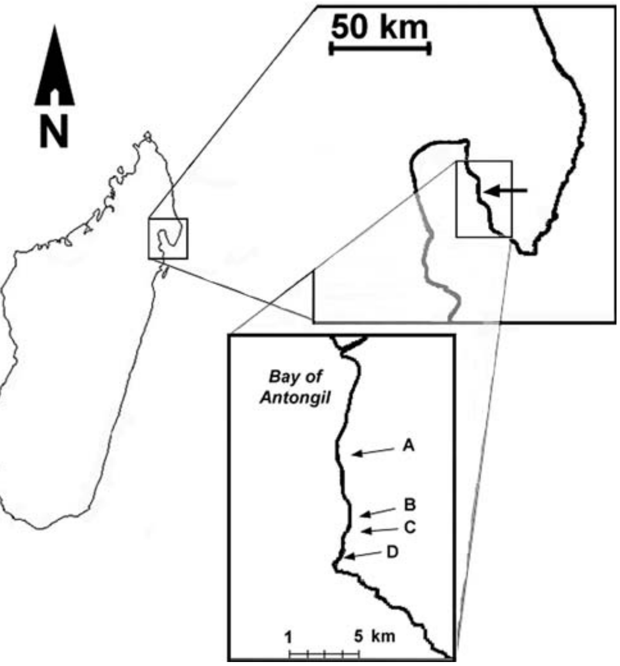

Fig. 1. Map of the study sites on the Masoala Peninsula, Madagascar. A = site east of Andranobe (Icos I); B = site east of Ambodiforaha (Icos II); C = site of the canopy raft; D = base camp at Tampolo.

up to 30 m. The surveys included transects from Andranobe to Icos I (from 0 to 250 m above sea level) and from Ambodiforaha to Icos II (from 0 to 200 m above sea level). Phytotelmata were studied in detail by taking readings of the water (dissolved oxygen, conductivity, pH, temperature, volume, and depth), the hole dimensions, and the height above the ground. Also noted were the host plant species, the substrate type at the bottom, other inhabitants, and the orientation of the opening of the phytotelma with respect to the vertical plane. All freshly captured individuals were measured, sorted according to sex, and photographed to record their natural color and characteristics, before preserving them in 90% ethanol. Specimens of freshwater crabs were identified using the taxonomic keys provided by Cumberlidge and Sternberg (2002), while the sesarmids were identified using the keys of Crosnier (1965) and Serène and Soh (1970). Specimens were deposited in the zoological collection of Northern Michigan University (NMU).

Crabs collected from phytotelmata were found to belong to two species: *Malagasya antongilensis* (Rathbun, 1905) (family Potamonautidae) and *Labuanium gracilipes* (H. Milne Edwards, 1853) (family Sesarmidae). Both species had been previously described, but very little was known of the habitat preferences of these rare taxa.

Systematics

Superfamily Potamoidea Ortmann, 1896
Family Potamonautidae Bott, 1970
Malagasya antongilensis (Rathbun, 1905)

Potamon (*Parathelphusa*) *antongilensis* Rathbun, 1905: 265, 266, fig. 21, pl. 12, fig. 5.—Cumberlidge, 1998: 210.
Hydrothelphusa (*Acanthothelphusa*) *antongilensis*.—Bouvier, 1921: 52.
Thelphusa madagascariensis.—Balss, 1929: 254.—Balss, 1934: 520, pl. 1, fig. 1 [not *T. madagascariensis* A. Milne-Edwards, 1872].
Potamon (*Geothelphusa*) *antongilensis*.—Balss, 1929: 355, fig. 21.
Gecarcinautes antongilensis antongilensis Bott, 1965: 337, figs. 1–3, figs. 1–3; 338, pl. 1.
Gecarcinautes antongilensis vondrozi Bott, 1965: 338, pl. 1, figs. 4, 5.—Cumberlidge *et al*., 2002: 75.
Gecarcinautes antongilensis.—Ng and Takeda, 1994: 163.
Malagasya antongilensis.—Cumberlidge and Sternberg, 2002: 61, fig. 1E, 3E, 4E, 5E, 6E, 7I, J, 8I, 10C, D, 11F; Cumberlidge *et al*., 2004: 1138, 1139, fig. 3C, table 1.

Material Examined.—Madagascar. Subadult male (cw 15.8, cl 12.8 mm) (NMU R1 2.xi.2001A), collected from water-filled tree hole 3.0 m above forest floor, mid canopy forest, from canopy raft, Masoala National Park, Masoala peninsula, 2 November 2001, by D. B. Fenolio and M. E. Walvoord. Subadult male (cw 20, cl 16.3 mm) (NMU R4 3.xi.2001A), collected from water-filled tree hole 2.3 m above forest floor, mid canopy forest, from canopy raft, Masoala National Park, Masoala peninsula, 3 November 2001, by D. B. Fenolio and M. E. Walvoord. Subadult male (cw 17.3, cl 13.5 mm) (NMU R6B 3.xi.2001B). collected from *Ravenala* leaf axil, 0.5 m above forest floor, lower canopy forest, from Icos II, Ambodiforaha, Masoala peninsula, 3 November 2001, by D. B. Fenolio and M. E. Walvoord. Subadult male (cw 12, cl 10 mm) (NMU 35 4.xi.2001A), collected from tree hole 0.8 m above forest floor, lower canopy forest, from Icos I, Andranobe, Masoala peninsula, 4 November 2001, by D. B. Fenolio and M. E. Walvoord. Subadult male (cw 14.7, cl 11.6 mm) (NMU 29 4.xi.2001B), collected from water-filled tree hole 0.5 m above forest floor, lower canopy forest, from Icos I, Andranobe, Masoala peninsula, 4 November 2001, by D. B. Fenolio and M. E. Walvoord.

Diagnosis.—Carapace heart-shaped, distinctly elongated, anterolateral margin of carapace with row of sharp teeth; pterygostomial region of carapace sidewall with small sparse hairs; suborbital, subhepatic regions of carapace sidewall with fine granulations; third maxilliped exopod with long flagellum; third maxilliped ischium as wide as merus, ischium with deep vertical sulcus; third sternal sulcus s3/s4 straight, horizontal, completely crossing sternum; s6/s7 meeting a5/a6 junction; walking legs (p2–p5) elongated, slender; inner margin of propodus of p5 with distinct spines; abdomen of adult male triangular; adult size range between carapace widths 27.5 to 34 mm. For a full description see Cumberlidge and Sternberg (2002).

Color in Life.—The carapace color of *M. antongilensis* is uniformly dark brown, the ventral thoracic surface is light brown, and the abdomen is dark brown. The dorsal surface of the chelipeds (propodus, merus, and carpus) is brown, and the fingers are cream; the walking legs are uniformly dark brown except for contrasting white/cream distal propodi and dactyli, giving the impression of striking white/cream "ankle socks." This is the first report of the natural color of this species because all of the other specimens are in museum collections and are a uniform brown, having been kept in preservative for many years.

Distribution.—The type locality of *M. antongilensis* was recorded simply as Antongil, and is presumably on the land adjacent to Antongil Bay, which includes the northeastern coastal part of Toamasina Province and the Masoala peninsula. Elsewhere in Madagascar, *M. antongilensis* occurs in the forested highlands and lowlands of Toamasina and Fianarantsoa Provinces, as well as in the northwestern lowland coast of Antsiranana and Mahajanga Provinces. This species is not known from Antananarivo Province, and is absent from most of Toliara Province except for the forested highlands in the southeast of the province. The distribution of *M. antongilensis* was summarized by Cumberlidge and Sternberg (2002) and by Cumberlidge *et al*. (2004).

Ecology.—Before this study very little information was available concerning the ecology of *M. antongilensis*,

Table 1. Some characteristics of the phytotelmic microhabitats examined, including those occupied by the freshwater crab *Malagasya antongilensis* (Potamonautidae) from the rainforests of the Masoala National Park, Madagascar. Details of the water chemistry are provided for selected phytotelmata. S = Specimen collected (Yes or No), RAFT = canopy raft, Icos I and II = enclosed tree-house canopy shelters, DO = dissolved oxygen, Cond. = conductivity, Temp. = temperature, Vol. = volume, SA = surface area.

S	Type	Locality	Ground (m)	Layer	pH	DO	Cond. (micro S)	Temp. (°C)	Vol. (mL)	Hole SA (mm)	Depth (cm)	Substrate type
N	RAFT	tree hole	6.3	mid	—	—	—	—	—	—	—	—
Y	RAFT	tree hole	3.0	mid	5.97	0.00	331	23.2	855	110.0	35	—
Y	RAFT	tree hole	2.3	mid	5.82	0.13	152.6	23.6	247.5	314.2	25	mulm
N	Icos I	tree hole	2.0	lower	—	—	—	—	—	—	—	—
N	RAFT	tree hole	1.5	lower	6.78	0.04	537	22.5	180	25.1	25	mulm
N	Icos I	tree hole	1.2	lower	5.11	0.13	203	25.5	200	125.7	12	mulm
N	Icos I	tree hole	1.0	lower	—	—	—	—	—	—	—	—
Y	Icos I	tree hole	0.8	lower	—	—	—	—	—	—	—	—
N	RAFT	tree hole	0.8	lower	5.54	0.29	81.3	22.5	45	37.7	—	—
N	Icos I	tree hole	0.7	lower	—	—	—	—	—	—	—	—
Y	Icos I	tree hole	0.5	lower	—	—	—	—	—	—	—	—
Y	Icos II	*Ravenala*	0.5	lower	—	—	—	—	—	22.0	3	mulm/leaves
N	Icos I	tree hole	0.4	lower	—	—	—	—	—	—	—	—
N	Icos I	*Ravenala*	0.2	lower	—	—	—	—	—	—	—	—
N	Icos I	tree hole	0.0	ground	4.90	0.07	201	20.6	250	263.9	12	mulm

because the museum specimens compiled over the last 100 years all lack ecological notes. The discovery of *M. antongilensis* living in phytotelmata in the lower and mid canopy forest levels includes the first record of any true freshwater crab living in a water-filled *Ravenala* leaf axil.

The transect surveys of 15 phytotelmata revealed five to be occupied by *M. antongilensis* (four water-filled tree holes and one *Ravenala* leaf axil) (Table 1). These phytotelmata were located on the transects between the coast and Icos units I and II, and near the canopy raft, at heights of up to 3 m above the forest floor in the lower and mid canopy layers of the forest. The physical characteristics of the water in the container microhabitats occupied by *M. antongilensis* are provided in Table 1. The water was warm (23.2–23.6°C), acidic (pH 5.82 to 5.97), low in oxygen (dissolved oxygen levels 0 to 0.13 ppm), and variable with respect to the levels of dissolved ions (conductivity 152.6–331 micro S).

Bayliss (2002) provided a detailed study of the ecological requirements of the phytotelmic East African freshwater crab *Potamonautes raybouldi* Cumberlidge and Vannini, 2004 (Potamonautidae) from Tanzania, and found that the water in crab-inhabited tree holes was slightly acidic (pH 6.1–6.6), oxygen depleted, and had a high mineral content. The reduced pH was attributed by that author to the decay of the leaves and organic debris that accumulated in the tree hole. Bayliss (2002) observed that crabs both removed leaf litter from the water and carried snails into the tree hole. These actions possibly served to both reduce the amount of leaf decay and to raise the calcium levels of the water so offsetting a larger reduction in pH. It is not known whether *M. antongilensis* uses container habitats mainly as temporary shelters, and feeds and breeds elsewhere, or whether these crabs spend significant parts of their life cycle in these containers. Interestingly, a second species of *Malagasya*, *M. goodmani* (Cumberlidge, Boyko, and Harvey, 2002) from the eastern lowland forests of the northern part of Toamasina Province (close to the Masoala Peninsula) is also found in container microhabitats, but in this case in the water-filled leaf axils of the screw pine *Pandanus* (Cumberlidge *et al*., 2002). Finally, the sesarmid *Scandarma lintou* Schubart, Liu, and Cuesta, 2003, from Taiwan is associated with the *Pandanus*, either hiding in the water-filled leaf axils or climbing on the leaves (Schubart *et al*., 2003).

Remarks.—Since its discovery, *Malagasya antongilensis* has been rarely encountered by biologists (perhaps due to its specialised habitat preferences), and as a consequence there are few literature reports, and very few specimens of *M. antongilensis* in museum collections. The thorough ecological report by Vuillemin (1972) of the ecology of a freshwater crab from northern Madagascar that she identified as "*Gecarcinautes antongilensis antongilensis*" is almost certainly misidentified, because the specimen pictured in that work clearly belongs to *Madagapotamon humberti* Bott, 1965. Indeed, the freshwater crabs of Madagascar as a whole are a taxonomically difficult group that has been relatively neglected over the years, and we are only now beginning to understand their true diversity and abundance (Bott 1965; Cumberlidge and Sternberg, 2002; Cumberlidge *et al*., 2004). What is known, however, is that endemism for the freshwater crabs in Madagascar is 100% at the species and genus level, and that many species (including *M. antongilensis*) are extremely rare and are known only from a handful of specimens (Cumberlidge and Sternberg, 2002; Cumberlidge *et al*., 2004). The conservation status of *M. antongilensis* has not been formally evaluated, but it is likely that this species would warrant an IUCN red listing assessment of vulnerable (IUCN 2001), based on its specialized habitat requirements, its relatively narrow distribution, and its potentially low population levels.

Superfamily Grapsoidea MacLeay, 1838
Family Sesarmidae Dana, 1851
Labuanium gracilipes (H. Milne Edwards, 1853)

Sesarma gracilipes H. Milne Edwards, 1853: 182.—De Man, 1887: 663, 664.
Sesarma (*Sesarma*) *gracilipes* Rathbun, 1910: 309, pl. 3, figs. 1, 2.—Tesch, 1917: 154, 155.—Crosnier, 1965: 59–61, figs. 80, 87, 95, pl. III, fig. 2.
Labuanium gracilipes.—Serène and Soh, 1970: 402, 407.

Material Examined.—Madagascar. Subadult male (cw 18.5, cl 17.4 mm) (NMU OAC 6.xi.2001A), collected in water-filled leaf axil of *Pandanus*, 15 m above forest floor in upper canopy forest, from canopy sled, Tampolo,

Table 2. Some characteristics of the phytotelmic microhabitats examined, including those occupied by the mangrove crab *Labuanium gracilipes* (Sesarmidae) from the rainforests of Tampolo and the Masoala National Park, Madagascar. Details of the water chemistry are provided for selected phytotelmata. S = Specimen collected (Yes or No), RAFT = canopy raft, Icos I = enclosed tree-house canopy shelter, DO = dissolved oxygen, Cond. = conductivity, Temp. = temperature, Vol. = volume, SA = surface area.

S	Type	Locality	Ground (m)	Layer	pH	DO	Cond. (micro S)	Temp. (°C)	Vol. (mL)	Hole SA (mm)	Depth (cm)	Substrate type
Y	Tampolo	*Pandanus*	17.0	upper	—	—	—	—	—	—	—	—
Y	Tampolo	*Pandanus*	15.0	upper	—	—	—	—	—	—	—	—
Y	Tampolo	*Pandanus*	15.0	upper	—	—	—	—	—	—	—	—
N	Icos I	tree hole	1.5	lower	5.29	0.14	99.6	22.1	200	138.2	25	mulm
N	Icos I	tree hole	1.3	lower	6.12	0.00	2090	21.3	200	88.0	12	mulm
N	RAFT	tree hole	1.1	lower	—	—	—	—	—	—	—	—
N	Icos I	tree hole	0.9	lower	—	—	—	—	—	—	—	—
N	Icos I	tree hole	0.9	lower	—	—	—	—	—	—	—	—
N	Icos I	tree hole	0.3	lower	5.46	0.33	333	21.4	50	47.1	4	mulm
N	Icos I	tree hole	0.2	lower	—	—	—	—	—	—	—	—
N	Icos I	tree hole	0.2	lower	—	—	—	—	—	95.0	—	—
N	Icos I	tree hole	0.1	lower	4.97	0.14	84	22.7	140	113.1	7	mulm
N	Icos I	tree hole	0.0	ground	—	—	—	—	—	—	—	—
N	Icos I	tree hole	0.0	ground	—	—	—	—	—	—	—	—

Masoala peninsula, 6 November 2001, by M. E. Walvoord and D. B. Fenolio. Subadult male (cw 15.8, cl 12.8 mm) (NMU OAD 6.xi.2001B), collected in water-filled leaf axil of *Pandanus*, 15 m above forest floor in upper canopy forest, from canopy sled, Tampolo, Masoala peninsula, 6 November 2001, by M. E. Walvoord and D. B. Fenolio. Subadult female (cw 14.6, cl 13.8 mm) (NMU OAB 6.xi.2001C), collected in water-filled leaf axil of *Pandanus*, 17 m above forest floor in upper canopy forest, from canopy sled, Tampolo, Masoala peninsula, 6 November 2001, by M. E. Walvoord and D. B. Fenolio.

Diagnosis.—Carapace square-shaped, slightly broader than long with nearly straight lateral margins diverging slightly posteriorly; no marginal teeth behind exorbital tooth; basal antennular segment rounded, only slightly broader than long; epigastric lobes well developed; ambulatory legs (p2–p5) elongated, with dactyli as long as propodi; anterior and posterior margins of meri of p2–p5 not parallel, widest distally; male abdomen triangular, broad-based, telson narrow, finger-shaped; gonopod 1 relatively short and stout; distal segment of gonopod 2 long and thin. Adult size range beginning at a carapace width of 30 mm. For a full description of this species see Crosnier (1965).

Color in Life.—The carapace color of *L. gracilipes* is mostly dark brown/purple, the ventral thoracic surface is light brown, the dorsal surface of the chelipeds (propodus, merus, and carpus) is bright orange, the fingers are cream, and the walking legs (p2–p5) are uniformly light brown.

Distribution.—Northeast Madagascar, the southeast coast of Africa, and the Indian Ocean. *Labuanium gracilipes* is the westernmost member of this Indo-West Pacific genus. In Madagascar, besides the Masoala peninsula, *L. gracilipes* is also found at Ivontaka and Ile Sainte Marie (Crosnier, 1965).

Ecology.—The discovery that *L. gracilipes* is a tree-climbing species that inhabits phytotelmata high up in the forest canopy is the first such record for any sesarmid from Madagascar. Before this study, very little information was available concerning the ecology of *L. gracilipes*, despite its being known to taxonomists for almost 150 years. This is no doubt due to the fact that these specimens were collected from highly inaccessible parts of the forest canopy using a canopy sled dragged beneath a dirigible.

The survey of 14 phytotelmata revealed three containers (all in water-filled *Pandanus* leaf axils) that were occupied by *L. gracilipes* (Table 2). The occupied phytotelmata were all in the forest close to the base camp at Tampolo, at heights between 15 to 17 m above the forest floor in the upper canopy layer. It would be interesting to know whether *L. gracilipes* uses these container habitats as temporary shelters and feeds and breeds elsewhere, or whether these crabs spend significant parts of their life cycle in phytotelmata. The diet of *L. gracilipes* is also unknown, although earlier workers have speculated that phytotelmic sesarmids elsewhere in the world are mainly generalist detrivores that dissect particulate matter (see Kitching, 2000).

Remarks.—The most recent treatments of the sesarmids recognise a number of different families in the superfamily Grapsoidea, including the Sesarmidae (formerly the subfamily Sesarminae of the Grapsidae; for a revision of familial taxonomy see Guinot, 1978; Sternberg and Cumberlidge, 1998; Martin and Davis, 2001; Schubart *et al*., 2002). Accounts of the habitat and ecology of sesarmids are available for a number of species and indicate that the majority of sesarmids are semiterrestrial coastal species that typically live in burrows along the landward margins of mangrove forests, muddy river banks, marshes, and freshwater habitats (Hartnoll, 1964, 1969, 1975; Alexander and Ewer, 1969; Chace and Hobbs, 1969). The ecology of the 11 species of the Indo-West Pacific genus *Labuanium* is only now becoming known (Serène and Soh, 1970; Jeng *et al*., 2003; Ng and Liu, 2003) but it is clear that the genus includes at least four species of tree-climbers (*L. politum* (de Man, 1888); *L. trapezoideum* (H. Milne Edwards, 1837); *L. rotundatum* (Hess, 1865); and *L. scandens* Ng and Liu, 2003), the latter two of which are known to inhabit phytotelmata.

Discussion

Although brachyurans are a predominantly marine group, many occur in tropical freshwater habitats, and there are numerous terrestrial species, some of which are arboreal (Von Hagen, 1977; Burggren and McMahon, 1988). A growing number of tree-climbing crabs from different parts

Table 3. Summary of crabs known to live in phytotelmic microhabitats.

OLD WORLD			
True freshwater crabs			
[1]*Globonautes macropus* (Rathbun, 1898)	Globonautinae	West Africa	tree holes
[2]*Malagasya goodmani* (Cumberlidge, Boyko and Harvey, 2002)	Potamonautidae	Madagascar	*Pandanus* leaf axils
[3]*Malagasya antongilensis* (Rathbun, 1905)	Potamonautidae	Madagascar	rainforest, tree holes, *Ravenala* leaf axils
[4]*Potamonautes raybouldi* Cumberlidge and Vannini, 2004	Potamonautidae	East Africa	tree holes
[5]*Ceylonthelphusa scansor* Ng, 1995	Parathelphusidae	Sri Lanka	tree holes
[6]*Archipelothelphusa* sp. Ng, 1991	Parathelphusidae	Philippines	tree holes
[12]*Arachnothelphusa* sp. Ng, 1991	Parathelphusidae	Borneo	tree holes
Grapsoidea			
[7]*Geosesarma noduliferum* (Lenz, 1910)	Sesarmidae	Southeast Asia	*Colocasia* leaf axils
[3]*Labuanium gracilipes* (H. Milne Edwards, 1853)	Sesarmidae	Madagascar	*Pandanus* leaf axils
[8]*Labuanium rotundatum* (Hess, 1865)	Sesarmidae	Indo-West Pacific	tree holes
[8]*Labuanium scandens* Ng and Liu, 2003	Sesarmidae	Taiwan	*Pandanus*, coconut trees
[9]*Scandarma lindou* Schubart, Liu, and Cuesta, 2003	Sesarmidae	Taiwan	*Pandanus* leaf axils
NEW WORLD			
True freshwater crabs			
No phytotelmic species known	Trichodactylidae	Central and South America	
No phytotelmic species known	Pseudothelphusidae	Caribbean, Central and South America	
Grapsoidea			
[10]*Metopaulias depressus* Rathbun, 1896	Sesarmidae	Jamaica	bromeliad tanks
[11]*Sesarma angustipes* Dana, 1852	Sesarmidae	Brazil	bromeliad tanks

[1] Cumberlidge (1991, 1996 a, b); Cumberlidge and Sachs (1991, 2000); [2] Cumberlidge *et al.* (2002); [3] present study; [4] Cumberlidge and Vannini (2004); [5] Ng (1995); [6] Ng (1991a); [7] Ng (1988, 1995); [8] Ng and Liu (2003); [9] Schubart *et al.* (2003); [10] Hartnoll (1964); Von Hagen (1977); Diesel (1989, 1991); [11] Von Hagen (1977); [12] Ng (1991b).

of the world are now known to live in container habitats such as leaf axils, bromeliad tanks, and bamboo stumps. These crabs belong to three families: the Sesarmidae, Potamonautidae, and Parathelphusidae (Table 3). The phytotelmic sesarmids are found throughout the Old and New World subtropics and tropics (e.g., Thienemann, 1934; Hartnoll, 1964; Von Hagen, 1977; Diesel, 1989, 1991; Diesel and Schuh, 1993; Diesel and Schubart, 2000), while the phytotelmic freshwater crabs (families Potamonautidae and Parathelphusidae) are all found in the Old World (Cumberlidge, 1991, 1996a, b, 1999; Cumberlidge and Sachs, 1991, 2000; Ng, 1991a, b, 1995; Bayliss, 2002; Cumberlidge and Vannini, 2004). In Asia, phytotelmic freshwater crabs that inhabit water-filled holes in trees include *Archipelothelphusa* Bott, 1969 (Parathelphusidae) from the Phillipines (Ng, 1991a); *Arachnothelphusa* from Borneo (Ng, 1991b); and *Ceylonthelphusa scansor* Ng, 1995 (Parathelphusidae) from Sri Lanka (Ng, 1995). In Africa, phytotelmic freshwater crabs include *Globonautes macropus* Rathbun, 1898 (Globonautinae) from the Upper Guinea rainforests of West Africa (Cumberlidge, 1991, 1996a, b, 1999; Cumberlidge and Sachs, 1991, 2000); and *Potamonautes raybouldi* Cumberlidge and Vannini, 2004 (Bayliss, 2002; Cumberlidge and Vannini, 2004) from East Africa. Interestingly, phytotelmy has not been reported for any of the freshwater crabs from the New World belonging to the families Trichodactylidae and Pseudothelphusidae.

The demands of living in a phytotelmic habitat above the forest floor require that crab inhabitants be adapted for tree climbing, air breathing, water conservation, and reproduction. Species of true freshwater crabs that climb trees (e.g., *G. macropus*, *P. raybouldi*, and *C. scansor*) all have slender, elongated walking legs, as does the sesarmid *L. gracilipes*. All phytotelmic potamonautids and sesarmids can clearly survive out of water for long periods, and those that have been studied (Cumberlidge, 1991; Bayliss, 2002) have a well-developed capacity to breathe air. Further, all of these phytotelmic crabs have a modified life cycle that provides a great deal of independence from sea water, and involves either direct development (true freshwater crabs) or some degree of abbreviated development (sesarmids). Interestingly, Schubart *et al.* (2003) pointed out that sesarmids that produce large eggs (*Geosesarma*, *Metopaulias*, and *Sesarma*) complete their life cycle inland, whereas those that lay small eggs spend the larval phase of their life cycle in the sea. It is notable that species of Malagasy frogs of the endemic family Mantellidae are found in both water-filled tree holes and leaf axils of *Pandanus* and *Ravenala*, but like crabs, these amphibians may only shelter in phytotelmata and may actually breed elsewhere (Glaw and Vences, 1992; Vences *et al*., 1999; Kitching, 2000).

It is still a relatively rare occurrence to find any crab in a phytotelmic microhabitat. To date only some six out of the almost 1000 species of true freshwater crabs, and about seven species of sesarmids are known to be phytotelmic (Table 3). The present study underlines the importance of the need to increase collection efforts over a broad range of habitats in Madagascar, especially in the canopy of the relatively undisturbed forests of the more remote regions of this island where most groups of animals and plants are known to have a high rate of endemism (Kremen *et al*., 1999).

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