AUSTRALIAN RAINFOREST BIOGEOGRAPHY: IS THERE A RELICTUAL BEETLE FAUNA IN AN *ALLOSYNCARPIA* RAINFOREST REFUGIUM, ARNHEMLAND, NORTHERN TERITORY?

STEWART B. PECK

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It has been suggested that the *Allosyncarpia ternata* forests of western Arnhemland, Northern Territory, may be relictual and may be biotic refugia from Tertiary times. To explore the hypothesis, a study of the entire beetle fauna was made in an *A. ternata* forest in Podocarpus Canyon, a small, isolated refugial forest containing the richest recorded plant diversity in NT. At least 508 beetle species were found, belonging to 58 families and at least 318 genera. Only 47 could be named to species; new species and new records for NT were found; and most species are probably not described. Of the named species limited to rainforest, more have disjunct distributions shared with Queensland than with Western Australia. These range disjunctions can be interpreted as evidence of either long distance dispersal or fragmentation of broader former distributions. No taxa were found which seemed to be phylogenetic relicts. A total diversity of more than 2000 species of insects is calculated for the forest. It is concluded that the beetle fauna assembled itself by dispersal in Holocene times. It is not a relict (ancient) assemblage. Beetles and insects in general may be able to contribute more towards reconstructing the biogeographic history of Australia and the forest history of NT, but only when their taxonomy and distributions become better known. ❐ *Insecta, beetles, Allosyncarpia ternata, rainforest, refugia, Northern Territory.*

Stewart B. Peck, Department of Biology, Carleton University, Ottawa, Ontario, K1S 5B6, Canada (e-mail: stewart_peck@carleton.ca); 25 November 2001.

It is generally thought that rainforest was widely (and perhaps continuously) distributed across northern Australia in the early Tertiary, and persisted until the Miocene (Truswell, 1990). Climatic change in the late Tertiary and the greatly fluctuating climates of the Pleistocene and Holocene further partitioned the rainforest of northern Australia into numerous separate and small patches as habitat islands associated with permanent moisture, scattered across a vast expanse of mostly eucalypt-dominated woodland and savanna.

The rainforest (also called monsoonal vine forest) patches of the Northern Territory are now completely isolated from both those of northern Queensland (by the Gulf of Carpentaria and the arid treeless grasslands of the Barkly Tablelands of northwestern Queensland), and from those to the west in the Kimberley Region of Western Australia (except along the coastline, and by a few riverine gallery forests). All the rainforest patches in NT and WA are concentrated in regions with higher rainfall (more than 600 mm per year), and the patches decline in size, density, species richness, and complexity westwards (Kikkawa et al., 1981; Russell-Smith, 1991).

Through support of the National Rainforest Conservation Program there is now an extensive database on rainforest vegetation in the Northern Territory and Western Australia. However, there are few studies of the insect assemblages of these forests. Compared to rainforests elsewhere in the world, Australian monsoon and wet tropical rainforests are generally thought to have an impoverished insect fauna (Anderson & Majer, 1991; Reichle & Anderson, 1996). Naumann et al. (1991) found beetles and sphecid wasps to be less diverse in Kimberley rainforests than in adjacent savannah, and of lower diversity than in the rainforests in eastern Australia. In 8 Kimberley rainforest patches, the insects in general (Naumann et al., 1991) and ants in particular had low diversity and high species turnover between patches. Majer (1990) stated that ant faunas in northern Australian rainforests are low in diversity when compared to other tropical regions. The ant communities (Anderson & Majer, 1991) were judged to be *ad hoc* assemblages of broadly-adapted species, with only a few specialist rainforest taxa.

NT RAINFORESTS. There are two distinct types of closed canopy rainforest in the Northern Territory (Bowman et al., 1991; Wilson et al., 1991). These are categorised as 'wet' and 'dry' monsoon forests (Russell-Smith, 1991). Both categories show a relationship between environment and floristic composition. The wet forests, of interest here, are a mixed species monsoon vine-thicket or forest, with many plant species having a disjunct distribution with Queensland, New Guinea and Indonesia. Most of the tree species have large seeds which are probably dispersed in part by birds. This forest commonly occurs on permanently moist to wet alluvial soils in low relief landscapes. A distinct subtype of closed canopy forest is dominated by the tree *Allosyncarpia ternata* S.T. Blake (Myrtaceae) and such forests span a gradient from wet to dry climatic zones. Although the wet forest types occur mostly in small and disjunct patches, there is evidence that significant gene flow exists between patches in most species of trees via pollen or vertebrate-dispersed seeds (Russell-Smith & Lee, 1992). In contrast, the seeds of *A. ternata* are very poorly dispersed (Bowman, 1991).

ALLOSYNCARPIA FORESTS. *Allosyncarpia ternata* is a fire-sensitive evergreen sclerophyll tree with a very limited distribution. It is endemic to western Arnhemland and adjacent Kakadu NP, and is largely restricted to sheltered gorges and rugged rock-strewn terrain where it is protected from fire (Bowman,1991). This tree dominates the closed-canopy rainforests in this sandstone terrain. The genus contains only this single species and its total distribution is 12-14°S and 132-134°30'E. *Allosyncarpia* forest constitutes 41% of all rainforest in N and NW Australia (Bowman, 2000). Its distribution and vegetational diversity is documented in Russell-Smith et al. (1993).

It has been suggested that this type of rainforest may be of ancient origin (Bowman, 2000). There are several lines of evidence for this idea. First, it occurs only on the western edge of the Arnhemland Plateau, which has continuously been a subaerial erosional landscape since the late Cretaceous. Second, phylogenetic relationships of *Allosyncarpia* are with genera occurring on land masses derived from Gondwanaland rift fragments (e.g. New Caledonia). This means that stocks ancestral to these genera were separated at least in the late Cretaceous (Russell-Smith et al., 1993). *Allosyncarpia* is significantly basal to the *Eucalyptus* clade, and *Allosyncarpia* forests are conceivably a relict of late Cretaceous and early Tertiary Australian closed forests (Bowman, 2000).

Biogeographic history of these forests is poorly understood. Only at Riversleigh, Queensland (Archer et al., 1989) do we have direct data on Tertiary vertebrate and plant macrofossils of rainforest habitat in northern Australia. In contrast, there is fairly good plant macrofossil or palynological data elsewhere in Australia for the late Cretaceous, Tertiary and Pleistocene (Trusswell, 1990). The gross biogeographic history of N Australian forests has thus been reconstructed from scant indirect animal data and scant direct plant evidence.

The forest considered in this study is in a remote, deeply-incised E – W gorge in the catchment of the East Alligator River, 32.5 km E of Jabiru, 12°87'73"S, 133°26'73"E. The site contains more rare plant species and greater total species diversity of gymnosperms and angiosperms than any other site in the Northern Territory; it also has the largest population of an endemic, highly restricted, and undescribed conifer (*Podocarpus* sp.) (Russell-Smith et al., 1993). The site is commonly called 'Podocarpus Canyon'. The extreme spatial restriction of this *Podocarpus* and many other rare rainforest taxa strongly suggests that the site is a biotic refugium and that relictual invertebrates might be present.

As part of a study of beetle species diversity and distribution in 10 separate NT rainforests, the *Allosyncarpia ternata* forest refugium of Podocarpus Canyon was sampled in detail. Beetles were chosen because of their abundance and diversity in forest systems, and because their patterns may be characteristic of those of insects in general. The purpose of this report is to give results, analysis and interpretation of the beetles found at Podocarpus Canyon. The goal was to determine if any beetle species are endemic or disjunct in this forest, and if this part of the insect fauna has a distinctive relictual or refugial character. Broadly speaking, the question is: can beetles resolve questions about the historical and ecological biogeography of this ancient rainforest type, which is now relictual and restricted to a very limited area in the NT?

MATERIALS AND METHODS

A rare opportunity combining permits and logistic support from the Conservation Commission of the Northern Territory allowed placement of insect traps in Podocarpus Canyon on 15 December and their retrieval on 23

December, 1993. Beetles were sampled by standard methods; using ultra-violet light traps, a malaise trap, 60 unbaited pitfall traps and 6 flight intercept traps. Flight intercept traps are not yet widely known. They are 2m long black fabric screens into which beetles fly, and then fall into troughs or pans containing a glycol preservative (Peck & Davies, 1980). These are extremely productive and efficient sampling devices for crepuscular and nocturnal beetles, especially in the Staphylinoidea. The dense canopy of the forest eliminates herbaceous and shrub vegetation on the forest floor. Standard sampling of low vegetation by beating and sweeping in the forest understory was not possible.

Identifications of the beetles were by the author or taxonomic specialists. Voucher specimens are in the collections of the Australian National Insect Collection, Canberra and the The Canadian Museum of Nature, Aylmer, Quebec. Data on habitat preferences and distributions for named species were sought in taxonomic papers, Naumann et al. (1991) or the Zoological Catalogue of Australia.

Insects present several possible broad distributional patterns which may suggest the history of a particular forest. In Australia general patterns of Australian insect zoogeography are known (Cranston & Naumann, 1991) as are broad zoogeographic patterns of beetle distributions (Howden, 1981). The following criteria were applied in seeking species judged to be useful in a historical biogeographic context.

1) Beetle species that occur in both rainforest and eucalypt woodland can probably easily move between separate rainforest patches. These species are of little value for the present study. Species known only from rainforests are the ones that have information value for this study.

2) Species exclusive to rainforest and found in either or both Queensland and WA as well as NT forests and which are disjunct between these areas may suggest either (1) fragmentation of formerly continuous rainforest distributions, or (2) late Pleistocene-Recent dispersal, perhaps through now-vanished forest corridors. Flightless species are most likely to have low dispersal potential, and to be evidence of range fragmentation.

3) Species limited to NT rainforests with sister species in Queensland or WA rainforest may suggest a common or continuous distribution in late Tertiary or early Pleistocene time, and this distribution was severed, allowing formation of the species pairs. Degree of differentiation between the pairs may be proportional to time of separation.

4) Unusual genera or phylogenetically relictual species may be indicative of a long period of isolation and of extinction of relatives, possibly caused by Tertiary-Pleistocene climatic change. It is necessary to differentiate between this and the possibility that the taxon is a relatively recent aerial arrival from the poorly known fauna of the Indo-Malay Archipelago.

RESULTS

DIVERSITY. A total of 58 families, and at least 318 genera and 508 species were taken. Most of the species are of small body size (5mm or less). Most of these proved to be in families and genera which are not yet taxonomically well studied in Australia in general, and in NT in particular. For most, only generic names could de determined (Appendix). Only 40 taxa could be named to species. These were generally species of larger body size, in the better known families such as Carabidae, Dytiscidae, and Scarabaeidae. Seven additional species were recognised as undescribed, and one of these has since been described (*Australoxenella wurrook* Storey & Howden, 1996). Undoubtedly a great many of the others, especially the smaller ones, are also undescribed species. These 47 recognised species are all generalist feeders, with no direct stenophagous association with individual plant species in the forest. No flightless species were found.

In terms of numbers of species and individual specimens, the most effective sampling methods were UV light traps (311 species and 3076 individuals) and flight interecept traps (215 species and 1418 individuals). Pit traps (27 species and 156 individuals) and malaise traps (23 species and 43 individuals) took an order of magnitude fewer species and individuals, but the sampling effort was not equivalent. All methods except malaise traps took species not sampled by other methods.

BIOGEOGRAPHIC PATTERNS. Forty seven species could be discriminated as named or new and are potentially informative. Of these, 35 were previously reported from NT, and 12 others of these were new species or species records for NT (Table 1). Thirty two species were previously known from Queensland, 16 from WA, 3 from New Guinea or the Oriental Region, and 11 with ranges into NSW or other states of Australia.

TABLE 1. Beetles from the *Allosyncarpia* rainforest in Podocarpus Canyon, Arnhemland, NT which could be identified to species, giving numbers of individuals by sampling method, and primary habitat and distribution data. A full list of all other taxa is in the appendix. Families according to Lawrence and Britton 1991, 1994. Column headings and abbreviations: Mal = malaise trap, Inter = flight intercept trap, Pit = unbaited pitfall trap, UV= uv light trap, Hab = known primary habitats for the species elsewhere: R = rainforest, S = open savannah woodlands; A = aquatic; Dist = distribution in other localities; NSW = New South Wales; NT = North Territory; NG = New Guinea and/or Oriental; Q = Queensland; WA = Western Australia; etc=additional states in Australia; * = new record for NT.

Taxon	Mal	Inter	Pit	UV	Hab	Dist
Suborder Adephaga						
Carabidae (data from Moore et al. (1987)						
Chlaenius flaviguttatus Macleay				1	R	NT, Q, etc
'Tachys' nervosus Slade				1	R	NT, Q, WA
Cratogaster sulcata Blanchard		28			R	NT
Lorostema bothriophora (Redtenbacher)			24		R	NT
Gnathaphanus whitei Slade				4	R	NT, Q
Pentagonica ruficollis S.G.				8	R	NT, Q, NG
Aephnidius adelioides Macleay				1	R	NT*, WA, Q, NG
Helluosoma atrum Castelnau				2	R	NT, Q
Holcoderus caerulipennis Slade				1	R	NT*, Q
Haliplidae (data from Lawrence et al. 1987, Larson 1994)						
Haliplus australis Clark				1	S	NT, Q, etc.
Dytiscidae (data from Lawrence et al. 1987, Larson 1994)						
Bidessodes flavosignatus (Zimm.)				1	S	NT, Q
Clypeodytes bifasciata Zimm.				5	S	NT, Q
Clypeodytes migrator (Sharp)				5	S	NT, Q, etc.
Copelatus bakewelli Balfour-Brown				59	S, R	NT, WA
Copelatus clarki Sharp				2	S, R	NT, Q
Hydaticus daemeli Sharp				2	S	NT, WA, Q
Hydroglyphus godeffroyi (Sharp)				3	S, R	NT, WA, Q
Hydrovatus ovalis Sharp				3	S	NT, Q
Platynectes decempunctatus (Fab.)				10	S, R	NT, WA, Q, etc.
Platynectes monostigma Hope				3	S	NT, WA, Q
Suborder Polyphaga						
Hydrophiloidea						
Hydrophilidae						
Sternolophus australis Watts				15	R, S	NT, WA, Q
Sternolophus marginicollis Hope				2	R, S	NT, WA, Q, etc.
Staphylinoidea						
Leiodidae						
Colenisia n. sp. 1		12	1	18	R	NT*
Colenisia n. sp. 2		1	1		R	NT*
Colenisia n. sp. 3				12	R	NT*
Colon n. sp.		7		4	R	NT*
Zeadalopus n. sp. 1		1			R	NT*
Zeadalopus n. sp. 2		4			R	NT*
Staphylinidae: Pselaphinae						
Eudranes carinatus Sharp		1			R, S	NT
Scarabaeiformia						
Scarabaeoidea (data from Houston 1992, Storey & Howden 1996)						
Lucanidae						
Figulus regularis Westwood			1		R	NT, WA, Q

TABLE 1 (*Cont.*)

Taxon	Mal	Inter	Pit	UV	Hab	Dist
Geotrupidae						
Australobolbus rotundatus (Hope)				1	R, S	NT, Q, NG
Hybosoridae						
Liparochrus infantus Petrovic				13	R, S	NT, Q
Lipchrus quadrimaculatus Harold				1	R	NT, Q
Scarabaeidae						
Ataenius occidentalis (Macleay)				8	R, S	NT*, WA
Aphodopsammobius rugicollis (Macleay)		2			R, S	NT*, WA
Coptodactyla lesnei Paulian		32	5	63	R, S	NT
Onthophagus latro Harold				2	R, S	NT, Q
Australoxenella wurrook Storey & Howden	8				R	NT*
Epholcis uniformis Britton				1	R, S	NT
Anoplostethus roseus Blanchard				31	R	NT, Q
Cryptodus obscurus Macleay				1	R, S	NT*, Q, etc.
Coccinellidae						
Scymnus mitior Blackburn					R, S	NT, WA, Q, etc
Tenebrionoidea						
Archeocrypticidae (data from Kaszab, 1984)						
Australenneboeus analis (Kaszab)				2	R, S	NT, Q, etc
Tenebrionidae						
Tanychilus pulcher Carter				1	R, S	NT, WA, Q
Curculionoidea						
Brentidae						
Schizoeupsalis promissus (Pascoe)				2	R, S	NT, Q, etc
Curculionidae: Scolytinae (data from Wood & Bright, 1992)						
Coccotrypes dactyliperda (Fabricius)		10	4	18	R, S	NT, WA, Q, etc.
Xyleborus perforans (Wollaston)			7	3	R, S	NT, WA, Q, etc.

Of 47 potentially informative species, 28 are known to occur in savanna habitats and are thus uninformative for this study. The remaining 19 species are known only from rainforest habitat. Of these, 9 are known only from NT, 10 also occur in Queensland, 3 also occur in WA, 2 in New Guinea, and 1 has a range extending into NSW or other states. These distributions most parsimoniously suggest ranges achieved by random dispersal in the Recent, from a centre of greatest diversity in Queensland. Of the 9 species known only from NT rainforests, their sister species are not known, and morphologically none seem to be phylogenetic relicts.

DISCUSSION

DIVERSITY. Darwin-Kakadu insect faunas have been the focus of previous studies (Britton, 1973; Kikkawa & Monteith, 1980) allowing Baehr (1992) to state that hygrophilous carabid beetles of N Australian refugia are as rich in Arnhemland as in N Queensland.

Naumann et al. (1991) reported 50 families, 191 genera, and 505 species of beetles from 8 Kimberley rainforest patches. Those results are difficult to compare with my study because samples were made in the dry season and by methods addditional to those used here. A maximum of only 78 beetles species were found in the richest single forest patch. The rainforests and adjacent savanna forests yielded a shared fauna of 35 families, 134 genera, and 250 species of beetles. The fauna exclusive to the savanna forests was 51 families, 235 genera, and 433 species of beetles. Thus, the savanna beetle fauna of the Kimberley in the dry season was appreciably more diverse than that of the rainforests. This is counter to generalisations that the highest species diversity occurs in rainforest habitats. Mares (1992) indicated that Neotropical mammal species diversity is also greatest in dryland habitats. I know of no comparative studies on diversity of Australian tropical savanna insects, but Andersen & Lonsdale (1990) eloquently elaborated on the importance of insects as the dominant herbivores in structuring the dynamics of Australian savannas.

In comparison to Kimberley rainforest patches, the beetle fauna of Podocarpus Canyon is apparently much more diverse. All Kimberley rainforest patches combined were species poorer than Podocarpus Canyon, but the sampling seasons were different. If the diversity of Podocarpus Canyon is less or comparable to that of the continuously humid rainforests of eastern Queensland is not yet known. No analysis is available for a Queensland rainforest beetle fauna for comparison. It is also not known to what extent the Podocarpus Canyon fauna is typical of NT rainforests in general or how it differs from that in adjacent savanna.

In a detailed species-level study on a part of the insect fauna of an NT rainforest patch, Andersen & Reichel (1994) found ants in Holmes Jungle, near Darwin, to be a more specialised rainforest fauna than that found in Kimberley rainforest patches. In NT rainforest ants in general, with 173 species in 46 genera, 27% are rainforest specialists, and some of these show distributional disjunctions, but none are endemic to NT rainforests (Reichel & Anderson, 1996). They also reported *Aphaenogaster* sp. B as unique to Podocarpus Canyon but this has since been found to be *Aphaenogaster pythia* Forel, a common Queensland species (Anderson pers. comm.).

It is frequently generalised that beetles may comprise 20-25% of the animal species diversity of any temperate or tropical terrestrial locality (Grove & Stork, 2000). Thus, Podocarpus Canyon, with over 500 beetle species, may possess as a minimum a total of 2000 insect species in the entire forest. In an elaborate and extensive study, Bassett & Arthington (1992) found 916 species of arthropods in 46000 specimens collected in flight intercept traps in the crowns of one species of rainforest tree in a 2 year study in N Queensland. The species were predominantly phytophagous. Ground dwelling and low-flying predators and scavengers were poorly represented. Davies & Margules (2000) reported 669 beetle species taken over several years in pittraps in eucalypt forests near Wog Wog, NSW. Allison et al. (1993) found 633 beetle species from 54 families by fogging 8 trees at 3 study sites in Papua New Guinea. These data support an estimate of a minimum diversity of 2000 insect species in the Podocarpus Canyon rainforest patch.

BIOGEOGRAPHY. Various studies have attempted to understand the biogeographic history of Australian forests through the distribution of the forest inhabitants. These have concluded that NTrainforests must have been more extensive in the past, being progressively fragmented and reduced to their present status of very small, disjunct remnants. Menkhorst & Woinarski (1992) and Bowman & Woinarski (1994) found that various mammal species use NT rainforest at least occasionally, but that no species is restricted to it. The NT rainforest mammal species are like those of the monsoon rainforest of the Kimberley but unlike those of the wet tropical forest of Cape York. Likewise, the NT monsoon rainforests also contain few obligate species of herpetofauna and there is more species similarity with the Kimberley than with Cape York (Gambold & Woinarski, 1993).

There is no direct evidence that the beetle assemblage contains any relictual or ancient components. The indirect evidence of the wide and disjunct distribution of most of the named species could be used to bolster either dispersal or range fragmentation arguments. The history of climatic change in NT and elsewhere in Australia in Pleistocene times is a dynamic one of alternating dry (glacial) and wet (interglacial) climates (Johnson et al., 1999). Porch & Elias (2000) summarised that these have sponsored many range shifts in beetles in Australia, but that distributional details and fossil documentation is lacking. Baehr (1992) accounted for the assembly of a rich diversity of hygrophilus carabid beetles in Arnhemland refugia through this mechanism of climatic change causing repeated range expansion and contraction.

CONCLUSIONS

A diverse beetle fauna inhabits the *Allosyncarpia* forest of Podocarpus Canyon. This study was able to segregate 58 families, and at least 318 genera and 508 species in samples of 4756 individual beetles. In spite of previous survey and taxonomic work, the beetle fauna of NT rainforests is still poorly known. Species level identifications were not generally possible. Few species could be named and their habitat preferences and distributions were not well enough known to be of use in constructing a numerically significant database for rigorously evaluating distributional patterns useful in interpreting past history of the forests. Whether or not phylogenetic and distributional patterns presented by a beetle fauna can contribute to understanding of the history of these forests is not yet evident.

Available evidence favors the interpretation that the *Allosyncarpia* rainforests are, in general, not static biotic assemblages which have remained relatively constant through long periods of time, but rather that they are dynamic plant assemblages. The present rainforest patches were formed through time by dispersal in a dynamic landscape shaped by climatic change, erosional deposition, and water table fluctuation (which is ultimately controlled by sea level) (Bowman, 2000). These processes have created a changing landscape in which conditions for the establishment of rainforest come and go through time. In light of this study and subjective impressions from fieldwork in other NT rainforests, I conclude that NT rainforest beetle faunas are fortuitous and changing assemblages. As such they will shed little light on understanding the history of the forests. Of more use will be actual beetle fossils and subfossils, which have proved to be so informative in interpreting Quaternary habitat change in north temperate countries (Porch & Elias, 2000). However, the extreme environment of NT is generally unfavorable for the preservation of such fossils.

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APPENDIX

Taxa and numbers of all individuals of beetles which could not be placed to named or new species category, found in *Allosyncarpia* rainforest in Podocarpus Canyon, Arnhemland, NT, by sampling method. Families according to Lawrence & Britten, 1991, 1994. Column headings and abbreviations: Mal = malaise trap, Inter = flight intercept trap, Pit = unbaited pitfall trap, UV = uv light trap.

Taxon	Mal	Inter	Pit	UV
Suborder Adephaga Carabidae (classification follows Moore et al. (1987) Callistitae				
Badister sp.				4
Scarititae				
Clivina sp. 1				1
Clivina sp. 2				2
Dischirius sp.				5
Trechitae				
Limnastis sp.				1
Tachys s.lat. sp. 1	1			
Tachys s.lat. sp. 2				2
Tachys s.lat. sp. 3				9
Tachys s.lat. sp. 4				31
Tachys s.lat. sp. 5				3
Tachyta sp.				5
Tachyninia genus sp.				3
Trechodes sp.				1
Pterostichitae				
Abacetus sp.				1
Loxandrus sp.				2
Morion sp.				1
Prosopogmus sp.				7
Perigonitae				
Perigona sp.				85
Harpalitae				
Acupalpus sp.				1
gen. 2, sp.				2
gen. 3, sp.				9
Hypharpax sp.				1
Notiobia sp.				2
Trichotichnus sp.				1
Oodini				
Coptocarpus sp.				1
Pentagonicitae				
Pentagonica sp.			1	15
Masoreitae				
Sarothrocrepis sp.				3
Lebiitae				
Agonocheila sp.				1
Anomotarus sp.			1	14
Helluodema sp.				
Minuthodes sp.				2
Parazuphium				1
Pogonoglossus sp.				2
Trigonothops sp.				4
Noteridae (classification from Lawrence et al. 1987, Larson 1994)				
Canthydrus sp. (new?)			5	
Hydrocoptus sp. (new?)			1	
Dytiscidae (classification from Lawrence et al. 1987, Larson 1994)				
Clypeodytes n.sp.			1	
Copelatus n.sp.			1	

Taxon	Mal	Inter	Pit	UV
Suborder Polyphaga Staphyliniformia Hydrophiloidea Hydrophilidae				
Anacaena sp.1			20	
Anacaena sp.2			14	
Berosus sp.			5	
Enochrus? sp.1			1	
Enochrus sp.2			1	
Enochrus sp.3			8	
Georissus sp.			11	
Globaria? sp.			1	
Helochares sp.1			2	
Helochares sp.2			6	
Hydrochus sp.			50	
Paracymus sp.			1	
Sperchus sp.			1	
Sphaeridinae gen.1 sp.1	2	1	4	
Sphaeridiinae gen.1 sp.2			1	
Histeridae				
nr. *Chlamydopsis (termitophilus)*		1		
Staphylinoidea Hydraenidae				
genus 1		2		151
Ptiliidae				
unsorted			61	
Scydmaenidae				
Coatesia sp.		1		
Genus l sp.1		115		6
Genus 1 sp.2		27		1
Genus 1 sp.3		32		59
Genus 1 sp.4		5		2
Genus 1 sp.5		5		3
Genus 1 sp.6		14		43
Genus 1 sp.7		5		15
Staphylinidae Tachyporinae				
Sepedophilus; 2 spp.				3
Aleocharinae				
Mesoporini gen. & sp.				1
Myllaena sp.		1		1
16 genera; 22 spp.			1	88
13 genera; 18 spp.				68
Osoriinae				
Osorius sp.				5
Oxytelinae				
Bledius; 7 spp.		22		271
Carpelimus; 7 spp.		44		60
Thinobius; 2 spp.				3
Thinodromus sp.		1		
Anotylus; 3 spp.		1		42
Euaesthetinae				
Edaphus; 2 spp.		6		5

Taxon	Mal	Inter	Pit	UV
Paederinae				
Cephalochetus sp.				3
Charichirus sp.		1		4
Dibelonetes sp.		1		
Lathrobium, 2 spp.				3
Lithocharis sp.			1	
Ochthephilum, 3 spp.				22
Pinobius sp.				2
Scopaeodracus sp.				3
Scopaeus, 2 spp.	1		6	
Stiliderus sp.	1			
Sunius, 2 spp.		11		5
Thinocharis sp.	1		1	
Oedichirus sp.				1
Palaminus sp.		1		
Pinophilus, 3 spp.				13
Staphylininae				
Diochus, 2 spp.		5		2
Hesperus sp.	1	100	8	9
Philonthus sp.				1
Acylophorus sp.			3	
Atanygnathus sp.	1		1	
Scaphidiinae				
Scaphisoma sp.	7		2	
Baeocera sp. 1		3		
Baeocera sp. 2		3		
Scaphobaeocera sp. 1		18		
Scaphobaeocera sp. 2		5		
Pselaphinae				
Bibloporellina n.gen.		7		
Brachyglutina n.gen. #1	4			
Brachyglutina n.gen. #3	1			
Brachyglutina n.gen. #5	1			
Brachyglutina n.gen. #6	1			
Bythinoplectini gen? #1	18			
Bythinoplectini gen? #2	1			
Bythinoplectini gen? #3	1			
Bythinoplectini gen? #4	1			
Bythinoplectini gen? #5	1			
Bythinoplectini gen? #6	1			
Clavigeropsis sp. 1		1		
Clavigeropsis sp. 2		46		
Clavigeropsis sp. 3		1		
Coryphomodes sp. 1		1		
Coryphomodes sp. 3		4		
Curculionellus sp. 2		4		
Curculionellus sp. 5		1		
Cyathiger sp. 1	7			
Durbos sp. 1		8		
Eupines sp. 1		2		
Eupines sp. 3		1		
Eupines sp. 4		1		
Eupines sp. 5		2		
Eupines sp. 6		1		
Eupines sp. 7		1		
Eupines sp. 8		2		
Eupines sp. 10		1		
Eupines sp. 11		1		
Eupines sp. 13		1		
Eupines sp. 14		3		
Eupines sp. 15		1		

Taxon	Mal	Inter	Pit	UV
Euplectini gen. #4		35		
Euplectini gen. B	1			
Euplectini gen. C	1			
Euplectus sp. 1	4			
Euplectus sp. 2	1			
Euplectus sp. 3	1			
Euplectus sp. 4	2			
Limoniates sp. 1	5			
Limoniates sp. 2	10			
nr. *Eupines* sp. 1	53			
nr. *Eupines* sp. 2	1			
nr. *Eupines* sp. 3	116			
nr. *Mesoplatus* sp. 1		2		
Palimbolus sp. 1	1			
Palimbolus sp. 2	2			
Pselaphaulax sp. 1		1		
Pselaphaulax sp. 2		3		
Pselaphaulax sp. 7		21		
Pselaphaulax sp. 10		1		
Pselaphaulax sp. 12		3		
Pselaphaulax sp. 13		2		
Pselaphaulax sp. 14		5		
Pselaphaulax sp. 15		6		
Tiracerus sp. 1	2			
Tiracerus sp. 2	1			
Tmesiphorus sp. 1		2		
Tmesiphorus sp. 3		1		
Tmesiphorus sp. 4		4		
Tmesiphorus sp. 5		1		
Tyraphus sp. 4		5		
Tyraphus sp. 5		1		
Scirtiformia Scirtoidea Scirtidae				
Cyphon sp.1		44		
Cyphon sp.2		4		15
Cyphon sp.3				1
Scirtes sp.1		1		
Eucinetidae				
Eucinetus sp.	1	17		19
Clambidae				
Clambus sp.		25		
Scarabaeiformia Scarabaeoidea (data from Houston 1992) Scarabaeidae Aphodiinae Eupariini				
Australammoecius sp.				1
Coprini				
Demarziella sp.		1		
Onthophagini				
Onthophagus sp.1		1		
Onthophagus sp.2			2	
Onthophagus sp.3				1
Onthophagus sp.4				1
Onthophagus sp.5		1		
Scarabaeini				
Lepanus sp.1		6		
Lepanus sp.2		1		
Sauvagesenella sp.				1

Taxon	Mal	Inter	Pit	UV
Melolothinae				
Automoliini				
Haplopsis sp.2				4
Liparetrini				
Colpochila sp.				1
Liparetrus sp.				1
Heteronycini				
Heteronyx sp. 1				21
Heteronyx sp. 2				1
Heteronyx sp. 3				2
Heteronyx sp. 4				3
Heteronyx sp. 5				1
Heteronyx sp. 6				27
Heteronyx sp. 7	1	6		81
Heteronyx sp. 8	1	2	1	3
Heteronyx sp. 9				12
Heteronyx sp. 10				2
Heteronyx sp. 11				1
Heteronyx sp. 12				6
Heteronyx sp. 13				11
Heteronyx sp. 14				1
Heteronyx sp. 15				5
Heteronyx sp. 16				1
Heteronyx sp. 17				3
Neoheteronyx sp.				3
Maechidiini				
Maechidius sp.	1	2		312
Melolonthini				
Lepidiota sp.1				4
Lepidiota sp.2				3
Genus 17				5
Elateriformia				
Byrrhoidea				
Limnichidae				
Byrrhinus sp. 1		1	1	105
Byrrhinus sp. 2				10
Byrrhinus sp. 3				5
'Limnichus' sp. 1		1	1	7
'Limnichus' sp. 2				5
Callirhipidae				
genus 1	3			34
Elateroidea				
Eucnemidae				
genus 1				1
genus 2				3
Throscidae				
Aulonothroscus sp. 1	1			1
Aulonothroscus sp. 2		1		
Aulonothroscus sp. 3		4		
Elateridae				
Agrypnus sp. 1				1
Agrypnus sp. 2				4
Agrypnus sp. 3				4
nr. *Antoligostethus* sp.				12
Augentos sp.				5
Conoderus sp. 1		9	1	
Conoderus sp. 2	8	7		
Conoderus sp. 3				16
Conoderus sp. 4				3
Conoderus sp. 5				3
Conoderus sp. 6				3

Taxon	Mal	Inter	Pit	UV
Conoderus sp. 7	1			
Paracardiophus sp.				20
Melanoxanthus sp. 1	2			167
Melanoxanthus sp. 2	1			
Melanoxanthus sp. 3				1
Pseudotetralobus sp.				6
genus 5		1		14
Lycidae				
genus 1 sp. 1				3
genus 1 sp. 2				3
genus 1 sp. 3				3
Lampyridae				
Pteroptyx ?sp.				3
Cantharidae				
genus 1 sp. 1				1
genus 2 sp. 1				3
Bostrichoidea				
Bostrichidae				
Xylobosca sp.				1
Anobiidae				
Dorcatoma sp. 1	1			1
Gastrallus sp.				4
Pronus? sp.				1
Cleroidea				
Trogossitidae				
Neaspis sp.		1		27
Cleridae				
Stigmatium sp.		1		
genus 2 sp. 1				2
Cucujoidea				
Sphindidae				
Aspidiphorus sp.	2			
Nitidulidae				
Carpophilus sp. 1	1			
Carpophilus sp. 2	1			
Cybocephalus sp.	2			
Lasiodactylus sp.		3	33	
Pallodes sp.			6	
Stelidota sp.		96	76	
Thylacrodes sp.	1		18	
genus 8			1	
Silvanidae				
Psammoecus sp.	4		1	
Silvanolomus sp.			1	
Laemophloeidae				
Placonotus sp.				1
Phalacridae				
Litochrus sp. 1	1			
Litochrus sp. 2				1
Litochrus sp. 3				4
Languriidae				
Cryptophilus sp.			99	
Erotylidae				
Episcaphula sp. 1			3	
Episcaphula sp. 2			12	
Thallis sp.				1
Bothrideridae				
genus 1			1	
Cerylonidae				
Cerylonopsis sp. 1		3		3
Cerylonopsis sp. 2		1		27

Taxon	Mal	Inter	Pit	UV
Endomychidae				
Holopatameans sp. 1				5
Corylophidae				
Anisomeristes sp.	23		11	
Lewisium? sp.		2		1
Orthoperus sp.	7			
Sericoderus sp.	15			
genus 5	2			
genus 6	8			
genus 7	5			
genus 8			1	
Lathridiidae				
Corticaria sp. 1	1	5		54
Corticaria sp. 2				5
Tenebrionoidea Mycetophagidae				
Litargus sp. 1	6	3		8
Ciidae				
Acanthocis sp. 1	1			
Cis pacificus group		1		
Mordellidae				
Glipostenoda ? sp.	5	3		15
Mordellistena sp.			6	
Zeamordella ? sp.	1			
genus 4			4	
Colydiidae				
Bolcocius sp.				6
Tenebrionidae Tenebrioninae				
Ectyche sp.			1	
Mesomorphus sp.			1	
Platydema sp. 1			4	
Platydema sp. 2			3	
Platydema sp. 3			2	
Platydema sp. 4			1	
Platydema sp. 5			2	
Toxicum sp.				1
Uloma sp.				5
genus 9			1	
Alleculinae				
nr. *Homotrysis* sp.				1
Nocar sp.		24	1	9
genus 1	7	3	15	
genus 3			3	
genus 4			1	
genus 5			6	
genus 6			1	
genus 8, unusual, claw not pectinate				2
Lagriinae				
Casnonidea sp.			1	
Salpingidae				
Lissodema? sp.			1	
Anthicidae				
Anthicus sp. 1				3
Anthicus sp. 2				1
Anthicus sp. 3				1
Anthicus sp. 4				1
Anthicus sp. 5				3
Anthicus sp. 6				1
Mecynotarsus sp.			1	
Aderidae				
genus 1		1	2	
genus 2	1			
genus 3			1	
genus 4			2	
genus 5			1	
genus 6			5	
Scraptiidae				
Scraptia sp.				1
Chrysomeloidea Cerambycidae				
Prosoplus sp.				1
Chrysomelidae				
Geloptera sp.				2
Longitarsus sp. 1	1			
Longitarsus sp. 2				1
Monolepta sp. 1	1			
Monolepta sp. 2	2			
Monolepta sp. 3				27
Monolepta sp. 4				12
Pepila sp.		1		
Rhyparida sp. 1	1			
Rhyparida sp. 2		1		78
Trachyaphthona sp.		1		
genus 4	1			
genus 12				3
Bruchinae				
Callosobruchus sp.				3
Curculionoidea Curculionidae Scolytinae (data from Wood & Bright, 1992)				
Cryphalus sp.				2
Scolytomimus sp.	1			
Cuculioninae				
genus 1	1	1	1	
genus 2	1	3		2
genus 3	1			5
genus 4	1			2
genus 5		3		
genus 6		1		
genus 7		4		
genus 8		1		
genus 9		1		
genus 12				3
genus 13				1
genus 14				1
Cossoninae				
genus 10		1		
genus 15				1
genus 16				1
Totals (including species data presented in Table 1):				
Number of species by sample method	23	215	27	311
Numbers of individuals by sample method	43	1,481	156	3,076
Totals: 58 families, minimally 318 genera, minimally 508 species				