PALAEODISTRIBUTION OF PYGMY-POSSUMS IN TASMANIA

by Jamie M. Harris and Jillian M. Garvey

(introduction)


This work is a contribution towards documenting the fossil distribution of the pygmy possums Cercartetus lepidus and C. nanus (Marsupialia: Burramyidae) in Tasmania. We provide locality data and bibliographic sources for 15 Quaternary fossil sites important for these species (i.e., Beeton Rockshelter on Badger Island, Cave Bay Cave on Hunter Island, Bone Cave, Derwent River Shelter 7, Kutikina Cave, Mackintosh Cave, Main Drain, March Fly Pot, Newdegate Cave, Nunamira, Ouse River Shelter 7, Parampar Meethaner, Pseudochelirus Cave, Warhol, and Warreen Caves on mainland Tasmania). Dates available for these sites span the period 3960 ± 60 to 34,790 ± 510 years ago. We also draw attention to a Late Oligocene fossil locality at Geilston Bay which produced an undescribed Cercartetus-like species. The recorded palaeodistribution of pygmy-possums in Tasmania is widespread, with sites on two offshore islands, and also in the southern, south western, and western areas of mainland Tasmania.

Key Words: Cercartetus, nanus, lepidus, Tasmania, distribution, fossil, Burramyidae.

INTRODUCTION

The eastern pygmy-possum Cercartetus nanus and little pygmy-possum C. lepidus are diminutive burramyid marsupials that occur in Tasmania (15–43 g and 6–9 g respectively; Strahan 1995). Modern Tasmanian records for C. lepidus and C. nanus indicate that both species are widely distributed (Rounsevell et al. 1991, Munks et al. 2004). However, the recorded modern Tasmanian range of C. lepidus is more extensive than that of C. nanus (see range maps in Munks et al. 2004). Differences in the distribution of these two species reflect both their biogeographical history and subtle differences in their ecological requirements. Most records for C. nanus in Tasmania are from wet forests/rainforests (Green 1973, Watts 1987), whilst those for C. lepidus are from more xeric communities including dry sclerophyll forests and heathlands (Green 1979, Wall 1985). However, in some areas of Tasmania the range and habitats of these species are reported to overlap.

Outside Tasmania, C. lepidus is found on Kangaroo Island, South Australia (SA) (Aitken 1967, 1974), south-east mainland SA (Aitken 1977) and north-west Victoria (Ward 1992, Menkhorst 1995). Cercartetus nanus is found as far north as southeast Queensland (Harris et al. in press), through parts of south-east coastal New South Wales (NSW) (Bowen & Goldingay 2000) and Victoria (Harris & Goldingay 2005a), and west to the southeast of SA (Cartwheel 2004, van Weenen & Harris 2006). On the mainland, the status of C. lepidus and C. nanus varies throughout their respective ranges from “Common” to “Vulnerable” (see Tulloch 2004). In Tasmania, the current status of both burramyids is recognised as “not threatened”, but this is based on incomplete information and is in need of review (Duncan & Taylor 2001, Munks et al. 2004).

A long-term perspective on the status and distribution of pygmy-possums can be gained by reference to information derived from their fossil occurrence in cave deposits. They are incorporated into the fossil record because several carnivorous marsupials and owl species prey on pygmy-possums (and other small mammals) and deposit bones in caves as scats or regurgitated pellets; and also because pygmy-possums are susceptible to some pitfall-style caves (see Harris & Goldingay 2005b). Caves provide excellent preservation sites for small mammal remains, and excavation and analysis at numerous cave sites in southern Australia have provided valuable information on past distribution patterns of mammalian species (e.g., Wakefield 1972, Archer 1974, Baynes 1987, Archer et al. 1991, Baird 1991, Baynes & Johnson 1996).

In the case of the mountain pygmy-possum Burramyis parvus, an assessment of its fossil distribution has shown a dramatic reduction in geographic range during the Late Pleistocene (Broome & Mansergh 1989, Brammall 1993, Mansergh & Broome 1994). A reduced distribution for C. lepidus is also apparent as fossil bones referable to this species have been discovered in areas where it is now extinct, i.e., in eastern NSW (Ride 1960) and eastern Victoria (Wakefield 1960). A preliminary investigation of the fossil occurrence of C. nanus in Victoria (Harris & Goldingay 2005b) suggested that this species has not undergone a broad contraction of geographic range like B. parvus or C. lepidus. Examination of the distribution of fossil sites in South Australia however, indicates a recent range contraction (Harris in press). At present, there is very little published information on pygmy-possum fossil remains from Tasmania, which limits current understanding of biogeographic patterns in the distribution of pygmy-possums through time across Australia. Hence, the aims of this contribution are: (i) to document available information on the fossil localities for pygmy-possums in Tasmania; (ii) plot the distribution of pygmy-possum fossil sites; and (iii) identify modes of accumulation involved at the various sites.

METHODS

The Southern Forests Archaeological Project (SFAP) CD (McWilliams et al. 1999), and several unpublished theses were examined with reference to pygmy-possum material.
recovered from Tasmanian archaeological cave sites. Records of Tasmanian fossil burramyids were also searched for in several journals including Australian Archaeology, Papers and Proceedings of the Royal Society of Tasmania, Tasmanian Cave and Karst Research Group Journal, and The Tasmanian Naturalist (Harris 2005). Several other published sources were also reviewed (see papers cited in Harris & Goldingay 2005b). Additionally, enquiries were made with the palaeontological divisions of the Australian Museum (AM), Sydney; Museum Victoria (MV), Melbourne; Queen Victoria Museum and Art Gallery (QVMAG), Launceston; and Tasmanian Museum and Art Gallery (TMAG), Hobart. Geographical information for identified fossil sites was obtained from the relevant literature, the Geoscience Australia online place-name search (https://www.ga.gov.au/map/names/), or directly from topographic maps. We also sought information from the Tasmanian Aboriginal Site Index (TASI), administered by the Department of Tourism, Parks, Heritage and the Arts (DTPHA) for the Tasmanian Aboriginal Land and Sea Council (TALSC), the Aboriginal Heritage Office, DTPHA, academic staff in the School of Zoology, University of Tasmania, and from members of the Southern Tasmanian Caverners Inc.

A multitude of taphonomic (preservation) biases can affect the abundance of pygmy-possums (and other small mammals) in cave sites. These include dietary selectivity, habitat preferences and physiological requirements of predatory accumulators, disparity in the ways that prey is eaten and digested, differential disappearance rates of prey remains, and variable accessibility of predator and prey populations (see Garvey 1999, Harris & Goldingay 2005b). Other factors include dispersal, scattering, or disintegration of bone due to gravity, stream wash, or the action of scavengers, including cave-trapped animals. Due to these and other biases operating inconsistently at the sites, we have not attempted to interpret stratigraphic data on the abundance of pygmy-possums, and have limited our investigation to reviewing whether Cercartetus material was reported as present/absent from the sites. This paper provides the first published list of known localities for fossil burramyids in Tasmania.

RESULTS

Material referable to Cercartetus has been reported from 15 Late Pleistocene and/or Holocene fossil sites in Tasmania (table 1). These include Cave Bay Cave on Hunter Island (Bowler 1974a, 1982, 1984) and Becton Rockshelter on Badger Island (Sim 1998), both to the north of mainland Tasmania (fig. 1). Pygmy-possum fossil and sub-fossil sites are also known from caves in the southern, southwestern and western areas of mainland Tasmania. The southern sites include Pseudocheirus Cave and March Fly Pot, which are two vertical caves in the Ida Bay karst, south of Lune River (Clarke 1988a, Muirhead 1990); Nunamira (formerly Bluff Cave) and Warhol (a vertical cave), both in the Florentine Valley section of the Junee-Florentine karst (Eberhard 1988, Cosgrove et al. 1990, Cosgrove 1991, 1996a, Cockbill 1999, McWilliams et al. 1999); and Newdegate Cave (H-1; formerly HX-7) in the Hastings karst, north of the Lune River (Clarke 1999, 2000). Southwestern sites are Bone Cave in the Weld River Valley (Northwood 1990, Allen 1996, McWilliams et al. 1999); Warrereen (formerly known as M86/2) in the Maxwell River Valley (Allen et al. 1989, Cockbill 1999, McWilliams et al. 1999), and Kutikina Cave (formerly Fraser Cave) on the Franklin River (Smith & Sharp 1993, Geering 1983, Jones et al. 1983, Kiernan et al. 1983; Jones 1990; Garvey 2006) (fig. 1). Sites in western Tasmania are Main Drain, a limestone cave at Bubs Hill, east of Queenstown (Clarke 1988b, 1989) and Mackintosh Cave on a tributary of the Pieman River (Stern & Marshall 1993, McWilliams et al. 1999). Sites outside these areas are the Ouse River Shelter 7 rockshelter (ORS 7) in the Shannon River Valley (Cosgrove et al. 1990, Cosgrove 1991, 1996b, McWilliams et al. 1999), Permerpar Meethaner rockshelter in the upper Forth Valley (Cosgrove 1995, 1999), and Derwent River Shelter 7 rockshelter (DRS 7) on the Derwent River (Garvey 1999).

Of particular significance for the antiquity of pygmy-possums is a Late Oligocene fossil locality at Gelston Bay (Tefford et al. 1975, Rich et al. 1982, Teford & Kemp 1998). A single right lower incisor collected from this site was the only identified remains of a species assignable to the family Burramyidae. The incisor was described by Teford & Kemp (1998:16) as "most similar to those of Cercartetus and Burramys, especially the former, although it is about twice the size of any living species of that genus". Further work may provide evidence to determine whether it is indeed a burramyid.

The literature pertaining to some of these sites provides information on counts of Minimum Number of Individuals (MNI) from different stratigraphic units. For example, for Cave Bay Cave, Bowdler (1984) reported a total of 52 C. nanus, with these being from the "Upper Midden" (MNI=25), "Sterile Layer" (MNI=10), "Lower Midden" (MNI=2), "Upper Pleistocene < 19,000 BP" (MNI=2) and "Lower Pleistocene ≥ 19,000 BP" (MNI=13). For C. lepidus, Bowdler (1984) reported that three specimens were collected, one from the "Lower Midden" and two from the "Lower Pleistocene ≥ 19,000 BP" unit. Clarke (1988b, 1989) recorded a single fragmented burramyid specimen from Main Drain, tentatively assigned to C. nanus. In the case of the two vertical caves at Ida Bay, there were two C. nanus and one C. lepidus retrieved from March Fly Pot, and for Pseudocheirus Cave there were 19 C. nanus and three C. lepidus retrieved (Muirhead 1990). For Warhol, Eberhard (1988) reported a single Cercartetus specimen that was cautiously assigned to C. lepidus.

In his study of the owl pellet remains from Newdegate Cave, Clarke (2000) recorded two specimens of both C. nanus (mandible and humerus) and C. lepidus (mandibles). For DRS 7, Garvey (1999) identified remains of C. nanus (MNI=26) and also some fragmentary remains attributed to Cercartetus sp. (MNI=8), which may have been either C. nanus or C. lepidus. For Permerpar Meethaner, counts of C. nanus specimens in the excavated material have not been published, but Cosgrove (1995:94) stated that this species was "identified in all sites". For Nunamira and ORS 7, Cosgrove (1991) presented preliminary stratigraphic data for Cercartetus spp., although these data have now been updated by the SFAP database (McWilliams et al. 1999). Similarly, preliminary counts of C. lepidus and C. nanus in several unpublished theses (i.e., Warrene—Cockbill 1999; Bone Cave—Northwood 1990) are also superseded by McWilliams et al. (1999).

The SFAP database currently contains records of Cercartetus material excavated from five caves in Tasmania (Bone Cave, Mackintosh, Nunamira, ORS 7 and Warren). For Bone Cave, two C. nanus left mandibles were recorded from Square B spit 2 (ID=29753) and Square B spit 3 (ID=29841). For Mackintosh, the database indicates that 11
<table>
<thead>
<tr>
<th>Site Name</th>
<th>Cl</th>
<th>Cn</th>
<th>Csp.</th>
<th>KI code</th>
<th>Site code</th>
<th>TASI code</th>
<th>Origin</th>
<th>Age (yr BP)</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Sources</th>
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<td>Cave Bay Cave</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>H1-XI</td>
<td>-</td>
<td>0031</td>
<td>MS, OP</td>
<td>22,750±20 to 18,550±600</td>
<td>40° 34' S</td>
<td>144° 45' E</td>
<td>Bowdler 1974a, 1982, 1984</td>
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<td>Beeton Rockshelter</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5558</td>
<td>MS, OP</td>
<td>23,180±1280</td>
<td>40° 18' S</td>
<td>147° 52' E</td>
<td>Sim 1998, Cosgrove 1999</td>
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<td>-</td>
<td>+</td>
<td>+</td>
<td>DRS7</td>
<td>4057</td>
<td>OP</td>
<td>3960 ± 60</td>
<td>42° 20' S</td>
<td>146° 44' E</td>
<td></td>
<td>Garvey 1999</td>
</tr>
<tr>
<td>Permerpar Meehaner</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>4434</td>
<td>MS, OP</td>
<td>33,850±450 to 33,280±420</td>
<td>41° 42' S</td>
<td>146° 05' E</td>
<td>Cosgrove 1995, 1999</td>
</tr>
<tr>
<td>Mackintosh Cave</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>LM90/1</td>
<td>4551</td>
<td>MS</td>
<td>17,030±31 to 14,820±140</td>
<td>41° 43' S</td>
<td>145° 40' E</td>
<td>McNiven et al. 1993, Stern &amp; Marshall 1993, McWilliams et al. 1999</td>
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<tr>
<td>ORS 7</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>ORS 7</td>
<td>2089</td>
<td>OP</td>
<td>30,840±880 to 2,450±70</td>
<td>42° 05' S</td>
<td>146° 50' E</td>
<td>Cosgrove et al. 1990, Cosgrove 1991, 1996b, McWilliams et al. 1999</td>
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<tr>
<td>Bone Cave</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1790</td>
<td>MS</td>
<td>29,000±520 to 13,700±860</td>
<td>42° 50' S</td>
<td>146° 27' E</td>
<td>Goede &amp; Bada 1985, Northwood 1990, McNiven et al. 1993, Allen 1996, McWilliams et al. 1999</td>
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<tr>
<td>Pseudocheirus Cave</td>
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<td>+</td>
<td>-</td>
<td>IB-97</td>
<td>-</td>
<td>OP, PF</td>
<td>12,800 to 400</td>
<td>43° 10' S</td>
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<td>Clarke 1988a, Muirhead 1990</td>
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<td>+</td>
<td>-</td>
<td>IB-46</td>
<td>-</td>
<td>PF</td>
<td>12,800 to 400</td>
<td>43° 10' S</td>
<td>146° 40' E</td>
<td>Muirhead 1990</td>
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<tr>
<td>Warhol</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>JF-392</td>
<td>-</td>
<td>PF</td>
<td>Holocene – Recent</td>
<td>42° 42' S</td>
<td>146° 30' E</td>
<td>Eberhard 1988</td>
<td></td>
</tr>
<tr>
<td>Main Drain</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>BH-8</td>
<td>-</td>
<td>PF</td>
<td>Holocene – Recent</td>
<td>42° 07' S</td>
<td>145° 46' E</td>
<td>Clarke 1988b, 1989</td>
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<tr>
<td>Newdegate Cave</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>H-1</td>
<td>-</td>
<td>OP</td>
<td>Holocene – Recent</td>
<td>43° 22' S</td>
<td>146° 50' E</td>
<td>Clarke 1999, 2000</td>
<td></td>
</tr>
<tr>
<td>Kotikina Cave</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>F-34</td>
<td>485</td>
<td>OP</td>
<td>19,770±850 to 14,840±930</td>
<td>42° 31' S</td>
<td>145° 46' E</td>
<td>Garvey 2006</td>
<td></td>
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<tr>
<td>Geilston Bay</td>
<td>-</td>
<td>-</td>
<td>?</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>23 Ma</td>
<td>42° 50' S</td>
<td>147° 21' E</td>
<td>Tedford &amp; Kemp 1998</td>
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</tr>
</tbody>
</table>

Cl = C. lepidus, Cn = C. nanus, Csp. = Cercartetus sp. KI code = Karst Index alphanumeric code assigned to the respective caves by the Australian Speleological Federation. Site Code = Identification codes assigned by individual research groups. TASI code = Tasmanian Aboriginal Site Index. Origin: OP = Owl Pellet, MS = Mammal Scat, PF = Pitfall. A dash (-) indicates that the data are unknown or not available. The age of the material is years before present (yr BP) provided by the source indicated. Ma = Millions of years ago.
bone fragments of Cercartetus spp. ("pygmy-possum; species unknown") were recorded. Cosgrove (1991) explained that no attempt was made to separate C. lepidus and C. nanus because of their similarity. Mackintosh Cercartetus material included mandibles, maxilla and long bones (humerus, radius, ulna, tibia), and were collected from squares/spits designated as HN7 (ID=1015, 1046, 1071; 1072; 1073), GO4 (ID=7455), HM13 (ID=10871) and GL5 (ID=1940; 1941; 1942; 1968). For Nunamira, the database contained 14 entries for "Cercartetus spp." representing 28 mandibles or maxillae (all from Square A1, Cell Z, spits 1-7, and Square B1, Cell W, spits 5-7). The Nunamira material is held by TALSC and recent examination of some of this collection allowed verification of the presence of both C. nanus and C. lepidus (J. Garvey unpubl. data). For ORS 7, only two mandibles of "Cercartetus spp." were recorded on the database, from Square B1, spit 6. For Warrean, there were 62 elemental specimens of C. lepidus, and 71 of C. nanus. The Warrean pygmy-possum bones excavated are mainly left and right mandibles, but also include various other skeletal elements. At Warrean, C. lepidus was collected from Square A (spits 11 and 16) and Square B (spits 32, 35, 42-45, 47-58, 60 and 61). The Warrean C. nanus was collected from Square A (spits 8, 10, 11-17, 19) and Square B (spits 32, 42, 46, 50, 52, 53, 55, 56, and 59) (see McWilliams et al. 1999).

Large mammal bones, particularly those of Macropus and Vombatus, were found in large numbers during archaeological studies of several of the caves referred to, and are thought to have been accumulated by humans (see Jones 1990, Cosgrove et al. 1990, Stern & Marshall 1993, Cosgrove 2002; Garvey 2006). However, owls and marsupial carnivores are the principal accumulators of the majority of small mammal species, notwithstanding that pitfalls have also accumulated significant numbers.

For Cave Bay Cave, Bowdler (1974b:698, 1984:88) attributed the accumulation of Cercartetus material (and also Antechinus and murids) to owls, "with the masked owl (Tyto novaehollandiae) considered the most likely candidate". Remains of larger mammals in this deposit were attributed to accumulation by Tasmanian devils (Sarcophilus harrisii), quolls (Dasyurus spp.) or humans. For Nunamira, Cosgrove (1991:260) stated that "the most likely source of [the small mammal] bone was regurgitated owl pellets", noting several hollows in the roof of Nunamira, which "would serve well as owl roosts". Cosgrove (1991) did not speculate on the identity of the owl species involved, but in subsequent publications it has been suggested that owls of the genus Tyto were responsible (e.g., McNiven et al. 1993).

For ORS 7, Cosgrove (1991:299) favoured owl predation as the most likely explanation for accumulation of Cercartetus and other small mammal remains because the bone was in "relatively good condition". For Warrean, owl-pellet bone is most common in the lower levels of the deposit (McNiven et al. 1993). For Bone Cave, fossil material recovered was highly fragmented and generally consistent with damage caused by marsupial carnivores (Northwood 1990, McNiven et al. 1993, Stern & Marshall 1993). Northwood (1990) believed that the eastern quoll Dasyurus viverrinus was responsible for the accumulation of small mammal remains in Bone Cave, which was supported by the discovery of D. viverrinus bones in the assemblage. Based on the size range of the bone fragments McNiven et al. (1993) agreed that D. viverrinus was primarily responsible, although it was noted that Sarcophilus harrisii may also have contributed some scat remains at this site. For Mackintosh Cave, Stern & Marshall (1993) implicated D. maculatus, stating that faunal composition and their relative abundances compared favourably with its diet. Further support for this conclusion came from the pattern of surface damage observed on the bones of the prey species, which was more characteristic of D. maculatus than it was of S. harrisii (also see Marshall & Cosgrove 1990). However, bones from larger prey species present in the assemblage may have been the result of the activity of S. harrisii (McNiven et al. 1993, Stern & Marshall 1993).

For Beeton Rockshelter, Sim (1998) suggested that most terrestrial bones recovered fitted the criteria for S. harrisii scat remains (following Marshall & Cosgrove 1990). However, Sim (1998:150) noted that the "murid and possibly other small mammal bones most probably originate from owls roosting and raptors perching in the shelter, although quolls may also be responsible for a component". At Permerjar Meethaner, most bone can be attributed to marsupial carnivore activity and this is supported by the discovery of old coprolitic material and of tooth marks on some bones. However, remains of smaller mammals in the lower portion were thought to be derived from owl pellet deposition (Cosgrove 1995). Warthol is a pitfall trap, and the small mammal remains present (including C. lepidus) are thought to have accumulated via an "abrupt shaft with vertical and overhanging walls" (Eberhard 1988:53). March Fly Pot was probably also a pitfall for Cercartetus (Muirhead 1990). The Cercartetus in Pseudocheirus Cave are thought to have been first accumulated by owls and then "washed from an owl deposit at a higher region of the cave before being deposited" (Muirhead 1990:18). However, this cave has nearly vertical walls, and because suitable owl roosting...
alocoves are absent, it is more likely these remains accumulated from pitfalls (A. Clarke pers. comm. 2006). At DRS 7, Garvey (1999) found that owls accumulated the small mammals, but post-depositional efforts prevented the identification of the species of owl.

The fossils from Badger Island (Beeton Rocksheke) and Hunter Island (Cave Bay Cave) are Late Pleistocene in age, dating to 24–21 ka (ka = thousand years ago) and 22–18 ka respectively (table 1). Most mainland Tasmanian sites for fossil pygmy-possums are also Late Pleistocene and span 35–12 ka, including bones collected from Warreene (35–15 ka), Perampera Meethaner (34–32 ka), Nunamira (32–12 ka), Bone Cave (30–13 ka), Kutikina Cave (20–14 ka) and Mackintosh Cave (16–15 ka). The ORS 7 site (31–2 ka) incorporated both Late Pleistocene and Holocene material. This is probably also true for March Fly Pot and Pseudoheiris Cave, which were inferred to be around 13–0.4 ka. There are also three undated deposits (Warhol, Main Drain, and Newdegate Cave) that are thought to be of Holocene to recent age. The other sites are the Holocene assemblage at DRS 7 (4 ka) and the Geelison Bay Oligocene material (~23 Ma).

**DISCUSSION**

With impacts of climate change on biota thought to be rapidly increasing (Hughes 2003), detailed understanding of prehistoric ranges is important, particularly for those species like *Burramy* that are suggested to be at risk of climate-induced extinction (Mansergh & Broome 1994). Of Tasmanian material that can be confidently assigned to *Cercartetus*, the dated ages range from 3900 ± 60 years (y) (DRS 7) to 34,790 ± 510 y (Warreene) (table 1). However, the reliability of the radiocarbon C14 dating (table 1) requires comment. The Cave Bay Cave date (22,750 ± 420 y) is one of a sequence of four dates between 14 and 23 ka that apparently agree well with stratigraphic and chronological evidence (Murray et al. 1980, Goede & Bada 1985). The series of dates for other sites are mostly, but not invariably, in stratigraphic order (see Cosgrove 1989, 1995, Stern & Marshall 1993, Jones 1995, Allen 1996). The concurrence of around 120 C14 dates across seven sites (McWilliams et al. 1999) suggests that the chronology is an accurate and robust reflection of events. Nevertheless, because C14 dating of samples can be subject to various errors (Goede & Bada 1985, Baynes 1999), all the dates reported here should be treated with caution. Corroboration with other dating methods, such as electron spin resonance (ESR), amino acid racemisation (AAR), thermo-luminescence (TL) and uranium-series (see Goede & Bada 1985, Prescott & Robertson 1997, Ayliffe & Veeh 1998, Grün et al. 2001) would impart greater confidence in these C14 dates.

**Identification of the predatory accumulators**

Several criteria have been established to differentiate an owl deposit from a mammalian carnivore deposit. In owl deposits the remains of small animals dominate; the largest animals are represented by juveniles; whole skulls and other skeletal elements are represented; and there is only modest fragmentation of the bone (see also Dodson & Wexlar 1979, Marshall 1986, Andrews 1990, Geering 1990, Kusmer 1990, Garvey 1999). In contrast, high fragmentation rates are characteristic of *S. harrisii* and *Dasypus* sp. coprolites (Marshall & Cosgrove 1990, Northwood 1990, Garvey 1999). Using these criteria, owls have been implicated as the main accumulator of small mammals at six sites — i.e., DRS 7, Kutikina Cave, Newdegate Cave, Nunamira, ORS 7 and Warreene (table 1). In contrast, at Mackintosh Cave and Bone Cave, mammalian predators were identified as the principal accumulators. At Cave Bay Cave, Beeton Rocksheke and Permerpa Meethaner, there is evidence for both avian and mammalian accumulators. However, identification of the specific predatory species involved at each of these cave sites remains ambiguous.

The Tasmanian Masked Owl *Tyto castanops*, Barn Owl *Tyto alba* and Southern Boobook *Ninox novaeseelandiae* can be nominated as possible avian accumulators, as these are the only owls known to have lived in Tasmania during the Late Holocene (Garvey 1999), and probably during the Late Pleistocene. Possible dasyurid accumulators were the Spotted-tailed Quoll *D. maculatus*, Eastern Quoll *D. viverrinus*, Tasmanian Devil *S. harrisii* and/or Tasmanian Tiger *Thylacinus cynocephalus*. Except for *T. cynocephalus*, there are numerous records for *Cercartetus* falling prey to these predators (see Guiler 1970, Wallis et al. 1977, Green et al. 1986, Mooney 1992, 1993, Mumbray 1992, Mc Nab et al. 2005). *Thylacinus cynocephalus* was a large predator, now believed extinct, which fed mainly on large animals such as kangaroos and wallabies (Menkhorst & Knight 2001). Hence, it seems reasonable to eliminate *T. cynocephalus* as the accumulator of the small mammal material in Tasmanian cave deposits on the basis that they were unlikely to take such small prey. Although it is possible that *N. novaeseelandiae* contributed a small amount of vertebrate bone to one or more assemblages, it is unlikely that this species was a significant contributor, probably because of its generally insectivorous diet. Precise identification of the predatory species involved at each of the cave sites referred to may be possible at a future date, by using microscopy to search for diagnostic taphonomic signatures such as digestive corrosion patterns or tooth markings, or by quantitative re-assessment of skeletal element representation and breakage (see also Northwood 1990, Garvey 1999, McWilliams et al. 1999, Harris & Goldingay 2005b). We also emphasise that further research is needed on the taphonomy of pitfall-originated *Cercartetus* remains, focusing particularly on identifying criteria which allow their differentiation from predator deposits.

**Past and present distribution of pygmy-possums in Tasmania**

The antiquity of the burramyid fossil record in Tasmania (Tedford & Kemp 1998) raises the intriguing possibility that pygmy-possums may have evolved in Tasmania and dispersed to mainland Australia. Conversely, members of this genus may have arrived in Tasmania via the mainland. If the latter hypothesis is correct, *Cercartetus* probably followed the same route as the Aboriginal Tasmanians — across exposed portions of a Bassian land bridge connecting Wilson’s Promontory, Flinders Island and northeast Tasmania (Cosgrove 1999). It is calculated that this bridge existed at 55–50 ka, and again at 37–31 ka and most recently at 29–12 ka (Blom 1988, Jones 1995, Cosgrove 1999). However, it is not known how long *Cercartetus* has resided in Tasmania and whether populations migrated during any or all of these alternating periods of land connection and isolation. Present evidence suggests that *C. nanus* and *C. lepidus* were both present in southwest
Tasmania as long ago as 35 ka (Warren). However, the oldest *Cercartetus* fossils from the mainland are dated to 279 ka (Cathedral Cave, at Naracoorte, in southeast SA; Reed & Bourne 2000, Harris in press). This raises questions concerning the palaeobiogeography and migration of this genus, but further data including re-assessment of radiocarbon dates are needed (see above).

Of particular relevance to future research is the effect of major climatic and vegetational changes in faunal associations in Tasmania during the Last Pleistocene (e.g., MacPhail 1975, Bowler et al. 1976, Colhoun 1978, Hope 1978, Jones 1984, 1990, 1995, Augustinas & Colhoun 1986, Cosgrove et al. 1990, Colhoun et al. 1991, Jordan et al. 1991, Kirkpatrick & Fowler 1998, Cosgrove 1999, Reid et al. 1999). Currently, based on palynological evidence, it appears that before 45 ka, the Tasmanian vegetation consisted mainly of alpine and subalpine taxa and the forested environments were confined to low altitudes. *Cercartetus* spp. do not tolerate terrestrial alpine and treeless subalpine habitats in Tasmania today (Kirkpatrick et al. 1993), and so may have had a restricted (or non-existent) distribution in Tasmania prior to 45 ka. Between 44 and 25 ka, the climate was still colder and wetter than today, but in this period *Cercartetus* is known from numerous sites from south-west Tasmania. *Cercartetus* appears to be present in the vicinity of several sites at the height of the last glacial (~18 ka), but populations were probably not abundant or widespread until the onset of warmer and wetter conditions at about 12 ka. The two species are widespread in the southwest region in modern times, with the habitat of *nanus* and other skeletal material requires specialist attention and assessment (see also Green & Rainbird 1983, Garvey 1999).

Excavations have taken place. Most of the sites are caves and there is a reflection of the distribution of cave sites where detailed excavations have taken place. Most of the sites are caves situated in the southern, southwestern, and western areas of Tasmania. In this region there are extensive tracts of karstic carbonate rock (mainly Silurian and Ordovician limestone and Cambrian/ Precambrian dolomites) and these older geological formations are apparently rare in the eastern regions of Tasmania, which may explain the relative paucity of *Cercartetus* fossils outside of the southwest. Obviously, the perceptible palaeodistribution of *Cercartetus* in Tasmania (and on mainland Australia) is restricted to suitable areas where conditions allow the preservation of delicate skeletal material (i.e., in caves and protected rockshelters), where stable climatic conditions prevail with near constant humidity. The collection of pygmy-possum material also requires careful excavation and small sieve sizes; otherwise their bones are likely to be lost (Hall 1975). They may be easily overlooked, especially when the focus of a fossil investigation is on larger taxa. Notwithstanding these potential sources of preservation and collection bias, comparison of Quaternary and present distributions suggest that there are apparently no regions where *Cercartetus* was, but is no longer, found on mainland Tasmania.

Our review of published literature indicates that pygmy-possums were not found among the mammal fossils excavated at a number of sites throughout Tasmania, including at Prion Beatus Rockshelter in far southern Tasmania (2070±70; Dunnett 1992); Flowerly Gully (7080±420; Gill 1968); Tiata Mara Kominya (formerly Beginners Luck Cave) (80,000 to 12,600±200; Goede et al. 1978, Murray 1979, Murray et al. 1980, Bowdler 1982, Allen 1996, Goede & Bada 1985); Pleisto Scene Cave (130,000 to 10,100±200; Murray & Goede 1977, Goede et al. 1978, Goede & Bada 1985); Cardia Cave (18,000; Jones & Allen 1984); Pallawa Trounta (formerly Acheron Cave) (29,800±720 to 13,000; McNiven et al. 1993, McWilliams et al. 1999); Maneeena Langatick Tattana Emita (10,250±420; Pocock 1992, 1993); Mannalargenna Cave (20,560±290 to 7,960±170; Brown 1993); Louisa Bay (Vanderwal 1979); Stone Cave (16,670±70; McWilliams et al. 1999); Wattarragga Rockshelter (10,910±110 to 410±60; McWilliams et al. 1999), or Titans Shelter (27 ka) (Goede & Murray 1979, Cosgrove et al. unpubl. data). The reason why burramyid bones were not reported from these caves is unknown. They may have been absent or too small to be detected in the excavations. The majority of these caves were used as roost sites for owls or den sites for dasyurids so it is expected that *Cercartetus* could be present. There are also a number of vertical (pitfall) caves with significant sub-fossil deposits of currently unstudied mammalian remains in the Bubs Hill, Cracroft, Hastings, Ida Bay, Junee-Florentine, Mole Creek, Mount Weld and Precipitous Bluff karst areas in Tasmania (A. Clarke pers. comm. 2006).

There are also many other caves known to contain mammal bone, but thus far only very small samples have been collected from the surface layers of these sites, and at present *Cercartetus* is not recorded. Such localities include Nanwoon Cave (7.2 ka); Main Cave, Montagu (13 ka); Boomer Cave (20 ka); Un-named Cave, Florentine Valley (97 ka); Nelson River Cave (19 ka); and Deena Reena Cave (19 ka) (Goede et al. 1978; Kiernan 1982; Goede & Bada 1985; Jones 1995; see also Andrews 1971). There are conservatively about 2800 other caves within Tasmania (Clarke 2005; see also Middleton 1979; Kiernan 1988; Jones 1995), but only a small number of these have been subjected to archaeological or palaeontological study.
CONCLUSION

This paper provides a preliminary account of Tasmanian burren-mid biogeography and highlights the need for more detailed palaeontological and archaeological study of caves and rockshelters throughout Tasmania. Further research should involve re-examination of the ORS 7 material to ascertain whether the *Cercartetus* specimens represent *C. lepidus*, *C. nanus*, or both species. Calculation of dates for the faunal assemblages from Warihoh, Main Drain and Newdegate Cave would also be desirable. The excavation of new localities is important because "new" fossil pygmy-possum material may be discovered, providing further information on the palaeodistribution of these species. Finding new fossil localities for *C. lepidus* and *C. nanus* in northwestern and northeastern Tasmania would be particularly valuable, as would Tasmanian cave deposits.

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