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A 48,000 year record of swiftlets (Aves: Apodidae) in North-western Borneo: Morphometric identifications and palaeoenvironmental implications

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ABSTRACT

This paper reports the results of an analysis of 508 sub-fossil carpometacarpi of swiftlets (Aves: Apodidae) recovered during archaeological excavations of the Great Cave of Niah in Sarawak, North-western Borneo. The bones date from 48 ky BP (ky BP: 10^3 calibrated years before present [1950]) to 0.35 ky BP and provide a means to consider populations of birds (of which one species is a significant commercial interest) in the context of environmental and climatic change in the past, and their responses to recent anthropogenic landscape changes in the present.

Biometric analyses and comparative data indicate that the collection contained specimens attributable to the three extant species of swiftlet that currently inhabit the Great Cave: the black-nest swiftlet (*Aerodramus maximus*), mossy-nest swiftlet (*Aerodramus salanganus*) and the white-bellied swiftlet (*Collocalia esculenta*). A subset of 267 identified specimens provides a time series that suggests that the Great Cave and environs have sustained populations of these three species throughout last 48,000 years. While changes in the wing length of extant species of swiftlet are known as a function of geographical and altitudinal range, statistical testing of a single character (greatest length of the carpometacarpus) did not indicate changes in wing length in any of the identified species.

The findings indicate that the local environs maintained a sufficient abundance of aerial arthropods to support populations of these obligate insectivores and are consistent with studies that suggest that the structural diversity of forest habitats was maintained throughout the late Pleistocene (48 ky BP to 11.6 ky BP) and Holocene (11.6 ky BP to 0.35 ky BP). The findings also provide context for the recent declines of the commercially-significant black-nest swiftlet and suggest that this species may be ill-equipped to adapt to recent anthropogenic deforestation of the Niah area.

1. Introduction

Analyses of bone assemblages can provide long timescale insights into the ecology of extant vertebrates and provide historical benchmark data for biological conservation (e.g. Jablonski and Sepkoski, 1996; Hunter, 1998; Lyman and Cannon, 2004; Lyman, 2006, 2012; Terry, 2009). This paper reports the results of an analysis of 508 sub-fossil carpometacarpi of swiftlets (Aves: Apodidae, Collocaliini) recovered during archaeological excavations of the Great Cave of Niah in Sarawak, North-western Borneo (e.g. Harrisson, 1967, 1970; Barker et al., 2007). The bones were recovered from sediments dating from 48 ky BP (ky BP: 10^3 calibrated years before present [1950]) to 0.35 ky BP.

The identification of species of swiftlet in the field is a considerable challenge (2000; Mayr, 1937, Chantler and Driessens; personal observation) and the classification and taxonomic affinities of species of swiftlet are poorly resolved issues (e.g. Moyle et al., 2008). Many aspects of molecular biology, physiology, ecology and behaviour have been proposed to inform on taxonomic affinities (e.g. Lee et al., 1996; Medway and Pye, 1977; Smythies and Davison, 1999; Chantler and Driessens, 2000; Thomassen et al., 2003; Price et al., 2004; Thomassen and Povel, 2006). While the debates are acknowledged, this study focused on a skeletal element from the wing and offers no commentary on taxonomy. The taxonomic conventions described in Thomassen et al. (2005) are followed throughout and the use of *Aerodramus* is retained (but see Thomassen et al., 2005, 275).

1.1. The Great Cave of Niah

The complex of caverns that form the Great Cave of Niah are located in an isolated outcrop to the northeast of the Gunung Subis limestone massif (3°48′–3°53′N, 113°49′–113°54′E, 15–397 m asl) in Niah National Park, ~15 km from the South China Sea (Fig. 1A,B). The National Park is a 31.4 km^2 island of lowland rainforest habitat that incorporates primary and secondary lowland dipterocarp forest with highly-adapted limestone forest growing on the karst (Hazebroek and Morshidi, 2006).

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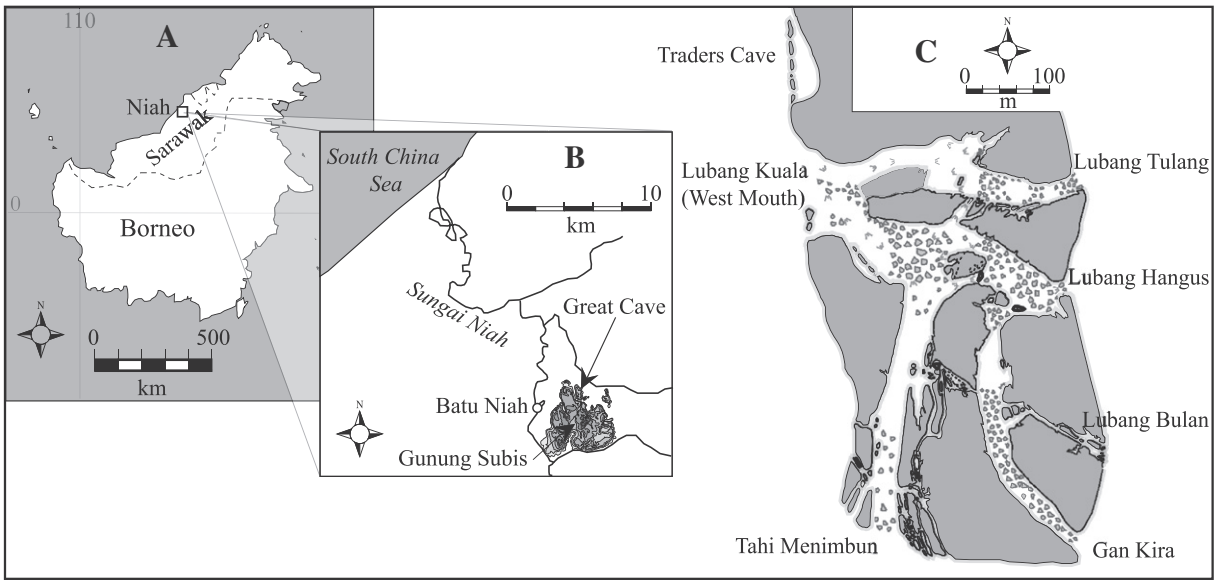

Fig. 1. (A) Location of Niah in Sarawak, North-western Borneo, (B) location of the Gunung Subis, and (C) plan of the Great Cave of Niah.

The Park is now surrounded by agricultural land that is mainly dedicated to the cultivation of oil palm (*Elaeis guineensis*) (Hansen, 2005).

The Great Cave is one of the most significant archaeological sites in Southeast Asia (e.g. Zuraina, 1982). The archaeological deposits of the West Mouth entrance (Fig. 1C) date from ~50 ky BP to the sub-recent (0.35 ky BP) and have yielded the earliest direct evidence (a human cranium) of the presence of anatomically modern humans in Borneo in the late Pleistocene, dated to 34–41 ky BP (Higham et al., 2009). The caverns of the Great Cave also became famous for their large, though now much reduced, populations of bats (Chiroptera) and swiftlets (Medway, 1962a, 1962b; Cranbrook, 1984; Leh and Kheng, 2001; Hall et al., 2002; Gausset, 2004).

1.2. Swiftlets

Palaeotropical swiftlets (genera *Aerodramus*, *Collocalia* and *Hydrochous*) are typically small, dark insectivorous birds (Fig. 2) distributed throughout Southeast Asia and the South Pacific. Like the larger swifts (Apodidae: *Apus* spp.), their torpedo-shaped bodies and high aspect ratio wings testify to a life spent on the wing (e.g. Videler, 2005).

Fig. 2. Black-nest swiftlet (*Aerodramus maximus*) with self-supporting nest adhered to cave wall.
Drawing by C.M. Stimpson from photographs.

Many species of swiftlet habitually nest in caves or cave-like structures and can form colonies of thousands of individual birds (Chantler and Driessens, 2000). Selected species are notable for their ability to navigate in darkness by the generation of echolocation clicks (e.g. Medway, 1967; Medway and Pye, 1977; Thomassen, 2005), a highly unusual ability in birds shared only with one other avian family: the neotropical oilbirds (Steatornithidae) (Suthers and Hector, 1985). This sensory adaptation has facilitated the colonisation of the cave interiors. The ability to echolocate in swiftlets was only associated with the genus *Aerodramus* until its discovery in a Philippine endemic, the pygmy swiftlet (*Collocalia troglodytes*), and now appears to have evolved at least twice among the swiftlets (Price et al., 2004). Six species of swiftlet are known to occur in Borneo and four species nest in caves (Table 1).

The nests of swiftlets incorporate a salivary secretion (a mucin-like glycoprotein) and in two cave-nesting species, the black-nest swiftlet (*Aerodramus maximus*) and white-nest swiftlet (*Aerodramus fuciphagus*), this secretion is highly prized as the principle component of a culinary delicacy: birds' nest soup (e.g. Lim and Cranbrook, 2002). Throughout Southeast Asia, birds' nest harvesting is a considerable economic endeavour and ecological concern (Cranbrook, 1984; Tompkins, 1999; Uning, 2001; Gausset, 2004).

Three species of swiftlet currently nest in the Great Cave (Table 1), where they occupy over 600 lubang (named roosting sites). The black-nest swiftlet and mossy-nest swiftlet (*Aerodramus salanganus*) are able to navigate by echolocation and establish colonies in the interior of the cave. The white-bellied swiftlet (*Collocalia esculenta*) does not echolocate and nests around the cave entrances in areas where sufficient light penetrates to permit visual navigation.

Table 1
Latin and English vernacular names of six species of Bornean swiftlet with notes on cave association and echolocation ability.

Species[a]	Common name	Cave nesting?	Echolocation?
Hydrochous gigas	Giant waterfall swiftlet	N	N
Aerodramus maximus	**Black-nest swiftlet**	Y	Y
Aerodramus fuciphagus	White-nest swiftlet	Y	Y
Aerodramus salanganus	**Mossy-nest swiftlet**	Y	Y
Collocalia esculenta	**White-bellied swiftlet**	Y	N
Collocalia dodgei	Bornean swiftlet	N	N

[a] Species of swiftlet that are currently recorded in the Great Cave are shown in bold.