



A new extinct dwarfed buffalo from Sulawesi and the evolution of the subgenus *Anoa*: An interdisciplinary perspective



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ABSTRACT

The fossil and extant faunas of Sulawesi, the largest island within the Wallacea biogeographic region, exhibit a high degree of endemism. The lowland anoa *Bubalus depressicornis* and the mountain anoa *Bubalus quarlesi*, two closely-related dwarfed buffaloes, are among the most peculiar endemic mammals of the region. Here, I describe a new species, *Bubalus grovesi*, from the Late Pleistocene/Holocene of South Sulawesi and I give a revised diagnosis of *Anoa*. *Bubalus grovesi* sp. nov. differs from all previously described *Bubalus* in both the size and proportions of the skeleton and in possessing a unique combination of discrete character states. Body mass estimates suggest an average mass of 117 kg for *Bubalus grovesi* sp. nov. and a body size reduction of about 90% with respect to a typical water buffalo.

A comprehensive overview of body mass estimates of dwarfed buffaloes and differences in their dental and postcranial features is included. Finally, new evidence on the taxonomy and island dwarfing of the anoas and available data from different disciplines are used to discuss the timing and mode of their evolution. The representatives of the subgenus *Anoa* would be dwarfed forms of the Asian water buffalo that arose following dispersal to Sulawesi during the Middle/Late Pleistocene.

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1. Introduction

Sulawesi, former Celebes, is the largest and possibly oldest island within the Wallacea biogeographic region (see e.g., Whitten et al., 2002). Its complex palaeogeographic history as a large oceanic island and crucial position at the biogeographic crossroads between East Asia and Australasia have resulted in high levels of endemism, particularly of the fauna (see e.g., Whitten et al., 2002; Cannon et al., 2007; Clough et al., 2010; Stelbrink et al., 2012). Several distinct forest types characterise Sulawesi's ecoregions and provide habitat for several endemic birds and the highest number of endemic mammals in Asia (Whitten et al., 1987).

The lowland anoa *Bubalus (Anoa) depressicornis* and the mountain anoa *Bubalus (Anoa) quarlesi*, two closely-related extant dwarfed buffaloes, are found only on Sulawesi and Buton Island (off the southeast coast) and they are among the most peculiar endemic mammals of the region (see e.g., Burton et al., 2005; Rozzi, 2014; Rozzi and Palombo, 2014). They are the smallest known extant Bovini, standing approximately 1 m tall at the shoulder and weighing up to 300 and 150 kg, respectively (Burton et al., 2005;

Lomolino et al., 2013). There is still much debate on the distribution and taxonomic status of the two species of anoa, although the classification of the subgenus *Anoa* within *Bubalus* is widely accepted and supported by recent morphological and genetic studies (Mohr, 1921; Bohlken, 1958; Dolan, 1965; Groves, 1969; Weise, 1979; Corbet and Hill, 1992; Wilson and Reeder, 1993; Kakoi et al., 1994; Schreiber and Nötzold, 1995; Kikkawa et al., 1997; Nowak, 1997; Pitra et al., 1997; Schreiber et al., 1999; Burton et al., 2005; Groves and Grubb, 2011; Rozzi, 2014; Rozzi and Palombo, 2014). The classification of the living anoas into two species, accepted by the majority of the specialists, is adopted here. The lowland and mountain anoas inhabit many types of forest, from lowland forest to montane forest at up to 2300 m above sea level, but, despite their common names, it is still uncertain whether the two species are sympatric or parapatric in their distribution (see, e.g., Burton et al., 2005). These species have no natural predators despite being frequently hunted by humans, while competitors include the endemic suids *Babyrousa celebensis* and *Sus celebensis*. Both anoas are classified as Endangered by the International Union for the Conservation of Nature (Semadi et al., 2008a, b), are included in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (UNEP-WCMC, 2011), and are legally protected under

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Indonesian law (see Rozzi, 2014 and references therein). Accordingly, any contribution towards a better understanding of the taxonomy and evolution of the subgenus *Anoa* is most valuable.

1.1. Remains of fossil and subfossil anoa

Since the beginning of the XXth century, several excavations have been carried out in the southwestern peninsula of Sulawesi, administratively designated as South Sulawesi, and many fossil vertebrates have been retrieved in the region, mainly by Swiss, Dutch and Australian-Indonesian scientists (for a detailed chronology of expeditions see e.g., Bartstra, 1977, 1997; Van den Bergh, 1999; Van den Bergh et al., 2001; Bulbeck, 2000, 2004; Bulbeck et al., 2000; Simons and Bulbeck, 2004). Fossil and subfossil remains of anoa have been recovered from two types of deposits: 1) Surface findings and colluvial/alluvial deposits along the Walanae river valley; and 2) Toalian cave sites (Fig. 1; see Van den Bergh, 1999; Simons and Bulbeck, 2004 and references in those papers; for the etymology of the term “Toalian” see Bartstra, 1997 and references therein). In both cases, available data suggest that representatives of the subgenus *Anoa* were part of the Sulawesi Sub-recent to Recent Faunas of Late Pleistocene to Holocene age (Hooijer, 1948, 1950, 1972; Clason, 1976; Groves, 1980; Van den Bergh et al., 2001). Additional evidence comes from local prehistoric art sites, such as the ones in the Maros karst and in the Bone region, including Late Pleistocene large naturalistic paintings of anoa and other endemic Sulawesian land mammals (see Fig. 1; Plagnes et al., 2003; Aubert et al., 2014; Tacon et al., 2014; Tan, 2014). Anoa are no longer present in South Sulawesi, although they are still living in other areas of the island (Semiadi et al., 2008a,

b). However, both species of anoa were believed to be present throughout the majority of the island’s forests in historical times (see Burton et al., 2005 and references therein).

Subfossil remains of anoa were first recovered in Toalian caves by Paul and Fritz Sarasin, the well-known Swiss naturalists, during their journeys of discovery through Sulawesi (Sarasin, 1905). The material, originally considered to belong to *Anoa depressicornis* by the Sarasins (Sarasin, 1905), was later assigned to *Anoa quarlesi* (described by Ouwens, 1910), because of its smaller size in comparison with the extant lowland species (Mohr, 1921; Hooijer, 1950).

Similar caves as the ones explored by the Sarasins were excavated by the Dutch archaeologist Pieter van Stein Callenfels in 1933–1934 and in 1937. The anoa remains retrieved from those caves were studied by Karel Willem Dammerman and ascribed to *Anoa depressicornis*. Dammerman (1939) did not find any significant difference in size between the molars of anoa collected by van Stein Callenfels and the ones of the larger living species.

In 1947, fossil remains of vertebrates and stone implements were found along the middle course of the Walanae river in South Sulawesi by the Dutch archaeologist Hendrik Robert Van Heekeren during his search for Pleistocene man (Bartstra, 1997). This collection of Pleistocene vertebrates was entrusted to the palaeontologist Dirk Albert Hooijer. Hooijer (1948) studied the material and identified some teeth of anoa collected near the village of Sompe as *Anoa depressicornis*. Scanty remains of fossil anoa were also collected by Van Heekeren at Celeko and Beru (personal observation in the collections of Naturalis Biodiversity Center) and in the Toalian cave site of Bola Batu (Hooijer, 1950). Additional material of *Anoa depressicornis*, recovered near Ciangkang and Calio by a joint

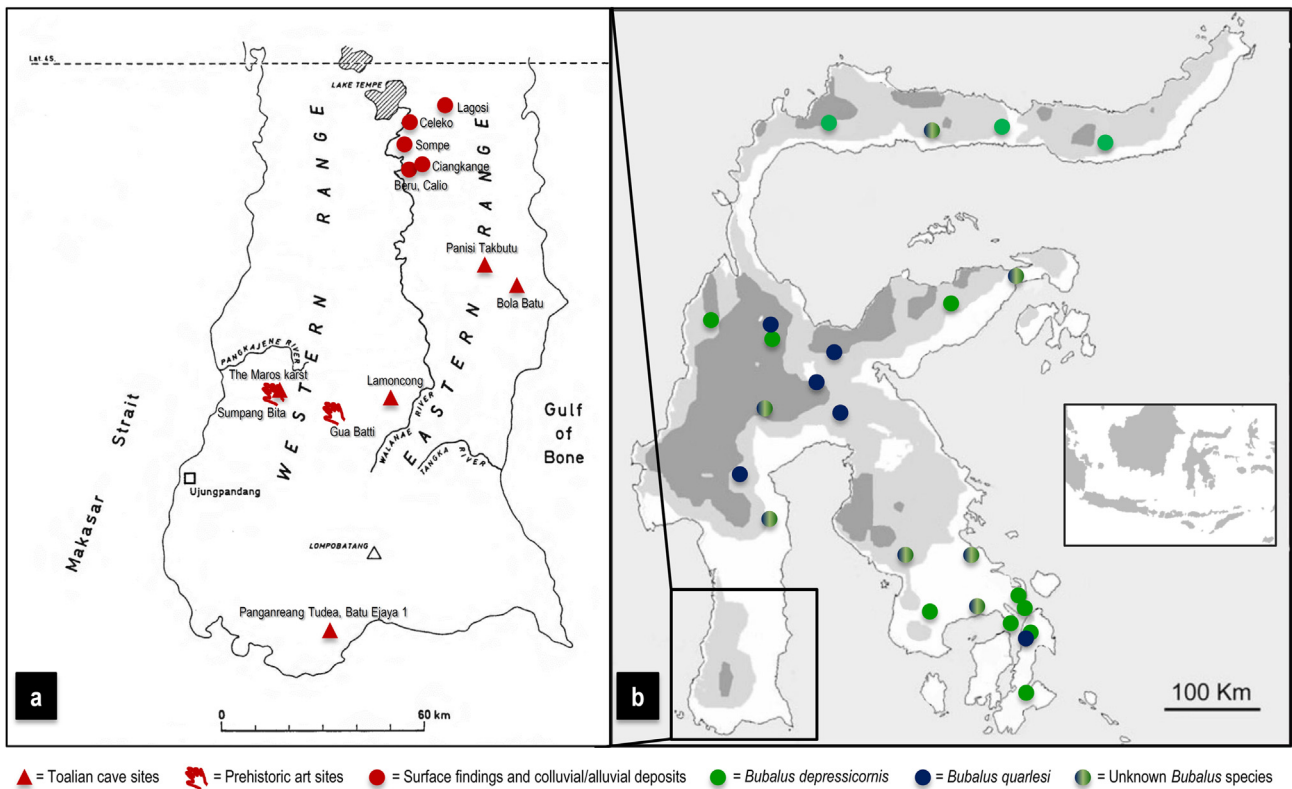


Fig. 1. Map of the main localities of fossil/subfossil anoa findings across South Sulawesi (a) and distribution of extant lowland, *Bubalus depressicornis*, and mountain, *Bubalus quarlesi*, anoas (b). The map symbols represent locations where data have been collected. Altitude key: white 0–200 m asl; light grey 200–1000 m asl; dark grey +1000 m asl. Altitude measured in metres above sea level. Modified from Bartstra (1977) and Burton et al. (2005).

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