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 anoa 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.

Keywords: anoa, body size, dwarfism, island evolution, Pleistocene, *Bubalus*

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 Nötzhold, 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 *Babyrusa celebensis* and *Sus celebensis*. Both anoas are classified as Endangered by the International Union for the Conservation of Nature (Semiadi 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 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 Subrecent 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 Sulawesi 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 in 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 Ciangkange and Calio by a joint Dutch-Indonesian expedition in 1970, was later described by the same author (Hooijer, 1972). While studying the material that new expeditions were bringing to light in the Walanae valley, Hooijer (1950) revised most of the mammalian remains that had been retrieved from Toalian sites in the first half of the XXth century. He ascribed the subfossil anoa remains found in Toalian caves to *Anoa depressicornis* and *Anoa quarlesi*, mainly on the basis of differences in size of teeth and postcranial bones (Hooijer, 1950). These taxonomic identifications were later included by Groves (1969) in his comprehensive review of the systematic status of the subgenus *Anoa*.

Since the late '60s, other expeditions have collected fossil and subfossil remains of anoa both along the Walanae valley (e.g., at Lagosi, at Paroto; see Van den Bergh 1999) and in Toalian caves (e.g., Leang Burung 2, excavated in 1969 by an Australian-Indonesian archaeological expedition to South Sulawesi, led by Ian Glover; see Glover, 1981; Clason, 1980, 1987; Simons and Bulbeck, 2004).

Although these recent investigations have been crucial in order to update the biochronology of the

Quaternary vertebrate fauna from Sulawesi (see below and Van den Bergh, 1999; Simons and Bulbeck, 2004), no morphological and taxonomic studies have been dedicated to the subgenus *Anoa* after the ones authored by Hooijer (1948, 1950, 1972) and Groves (1969). Here, I review the material studied by Hooijer, I give a revised diagnosis of *Anoa* and I describe a new species of *Bubalus* (*Anoa*) from the Late Pleistocene/Holocene of South Sulawesi. Furthermore, differences in dental and postcranial features among living and extinct dwarfed buffaloes are explored here for the first time. Finally, the available chronological framework and new data on the taxonomy and body size reduction of anoa are put in a broader palaeobiogeographical context and used to discuss the timing and mode of evolution of the subgenus.

2. Materials and methodology

The descriptions below are based on direct observations of the original specimens (teeth and postcranial bones) that were collected from various sites on South Sulawesi and are now housed at the Naturalis Biodiversity Center (Leiden, The Netherlands). Morphological comparisons were made with osteological specimens coming from several American and European museums: American Museum of Natural History (AMNH), The Field Museum of Natural History (FMNH), Smithsonian National Museum of Natural History (NMNH), Academy of Natural Sciences of Drexel University (ANSP), Natural History Museum (NHM). A list of the specimens in the study is provided in Appendix A. The osteological terminology used for the description of the specimens that constitutes the main subject of this study follows Hooijer (1948), Gentry (1992), and Rozzi (2010).

All measurements were recorded to the tenth of a millimeter, using a digital caliper. See Appendix B for abbreviations of measurements.

In order to infer the size shift of the new species of anoa and its living relatives in light of the island rule, their body masses were estimated by using the predictive equations with the lowest predictive

errors among those based on dimensions measurable on the available specimens (Appendix C), then averaging all the obtained body masses. Furthermore, the relative size of the focal island species was expressed as a proportion of the body mass of their putative mainland ancestor (S_i = body size divergence, *sensu* Lomolino, 2005).

Statistical analyses were performed using JMP (version 9; SAS Institute Inc., Cary, NC, 2009) software and Past (version 3.08; Hammer et al., 2001).

3. Systematics

Class MAMMALIA Linnaeus, 1758

Order ARTIODACTYLA Owen, 1848

Family BOVIDAE Gray, 1821

Tribe BOVINI Gray, 1821

Genus *BUBALUS* Hamilton-Smith, 1827

Subgenus *ANOA* Hamilton-Smith, 1827

Type Species: *Bubalus (Anoa) depressicornis* Hamilton-Smith, 1827

Revised Diagnosis: small-sized buffaloes; small horn cores, not curved and only slightly divergent; the parietal is less reduced than in *Bubalus (Bubalus)* and inclined at more of an angle to the occipital, less to the frontal; the occipital is higher, narrower; the supraoccipital has a greater antero-posterior and a smaller transverse extension on the upper surface of the skull than in *Bubalus (Bubalus)*; the auditory bullae are larger and the orbits are less prominent; the premaxilla extends back almost to the level of P2 and has a long union with the nasal; p2 is almost always absent; ectostylids (basal pillars, accessory outer columns) are generally present only in m1, although they may occasionally develop also in m2 and m3; the protoconid of p4 is gradually convex from back to front, instead of having a median outer rib marked off posteriorly – as in *Bubalus (Bubalus)*, so that the vertical groove between protoconid and hypoconid is V-shaped, less broad and less deep;

humerus with top corner of distal medial condyle markedly squared and not rounded as in *Bubalus* (*Bubalus*).

Remarks: the combination of peculiar features shown by the anoas make their phyletical relationships and their origin and evolution problematic to determine. According to Pilgrim (1939), *Anoa* shows some features in common with the Villafranchian ancestral genus *Hemibos*, and even with *Proamphibos*: for instance, simple horn cores and a similar shape and orientation of the parietal and occipital bones characterise all those taxa (Pilgrim, 1939; Groves, 1969). In particular, the occurrence of short, straight, simple (without keels or grooves) and uncompressed horn cores is generally regarded as a plesiomorphic feature in bovids and it is shared by several archaic genera (e.g., *Eotragus*, *Namacerus* and *Protragoceros*; see Rozzi, 2014; Rozzi and Palombo, 2014). Nevertheless, the acquisition of simple horn cores, and in a few cases straight and strongly inclined backwards, has also be regarded as an apomorphic feature resulting from the evolution under insular conditions. In fact, the simplification of the horn cores is one of the most recurring patterns in insular bovids and, according to Rozzi and Palombo (2014), it would have evolved in response to a decreased predatory pressure, a change in habitat and/or a body size reduction. In other words, the presence of simplified, conic, straight horn cores in the anoas would indicate that these apparently ‘archaic’ features actually correspond to apomorphic characters acquired during their evolution in an insular context. Furthermore, *Anoa* shares many specialised features with *Bubalus* and, although new differences in teeth and postcranial bones are described in the revised diagnosis above, they do not seem to justify a generic distinction. Indeed, the similarity between an adult individual of anoa and a young water buffalo is very striking in the skull and externally (Groves 1969). Accordingly, I agree with the majority of authors in considering *Anoa* as a subgenus within *Bubalus* (see, e.g., Bohlken, 1958; Dolan, 1965; Groves, 1969). This attribution is supported also by analyses of the anoas’ haemoglobin β chain amino acid sequences (Kakoi et al., 1994) and the cytochrome β region of their mtDNA (Tanaka et al., 1996). Likewise, the hypothesis that a representative of the genus *Bubalus* would be the ancestor of the *Anoa* seems supported by both morphological and genetic

evidence. However, results from different fields (genetics, archaeology, palaeontology) are not always in agreement with each other and make the investigation on the evolution of this subgenus extremely difficult (see discussion).

In addition to the extant lowland and mountain anoas (for a diagnosis see Groves, 1969 and Groves and Grubb, 2011), a new extinct species, described below, is included in the subgenus.

BUBALUS GROVESI, sp. nov.

(Figs. 2-7; Tables 1-3)

Anoa depressicornis Dammerman, 1939: 68-69.

Anoa depressicornis subsp. Hooijer, 1948: 1323-1325.

Anoa depressicornis Hooijer, 1950: 136-144.

Bubalus depressicornis Groves, 1969: 5-7, 9-10.

Anoa depressicornis Hooijer, 1972: 14.

Anoa sp. Simons and Bulbeck, 2004: 175-181, 183.

Holotype: RGM.1317470, partial right metacarpal (Figs. 2, 5; Table 2). Specimen collected by Pieter van Stein Callenfels in 1934 and housed within the Dubois collection of the Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie and Rijksmuseum van Geologie en Mineralogie).

Type Locality: Leang Tomatoa Kacicang, a rockshelter north of Cani (= Tjani; see Dammerman, 1939; Hooijer, 1950; Van Heekeren, 1972), in the Lamoncong area.

Referred material: one P3/P4 (RGM.1317472), two M1/M2 (RGM.1317474, RGM.1317475), one M3 (RGM.1317476), one p4 (RGM.1317473), two m1/m2 (RGM.1317477, RGM.1317478), and two partial right metacarpals (RGM.1317469, RGM.1317471) from Leang Tomatoa Kacicang, Lamoncong area; four M1/M2 (RGM.1317489, RGM.1317490, RGM.1317491, RGM.1317492), three m1/m2 (RGM.1317493, RGM.1317494, RGM.1317495), one m3 (RGM.1317496), one

partial right humerus (RGM.1317484), one right astragalus (RGM.1317485), one right calcaneum (RGM.1317486), one partial metatarsal (RGM.1317487), and one intermediate phalanx (RGM.1317488) from Pangareang Tudea (levels C-D), south coast of South Sulawesi; one M1/M2 (RGM.1317482), one m3 (RGM.1317483), one proximal phalanx (RGM.1317479), one intermediate phalanx (RGM.1317480), and one distal phalanx (RGM.1317481) from Pangareang Tudea (levels A-B), south coast of South Sulawesi; one dental series (p4-m3; RGM.1317497) from Sompe, Sopeng district; one M3 (RGM.1317468) from Ciangkange, south of the Cabenge-Pampanua road; one M1/M2 (RGM.1317466) from Beru; one M1/M2 (RGM.1317467) from Celeko.

Diagnosis and differential diagnosis: A dwarfed buffalo of smaller size on most measurements than the species of the subgenus *Bubalus* (e.g., *B. arnee*, *B. mindorensis*, *B. cebuensis*), but larger than the two living anoas (*B. depressicornis* and *B. quarlesi*). The humerus, metapodials, calcaneum, astragalus and teeth display a mixture of characters shared with *Bubalus* (*Bubalus*) (e.g., humerus with pronounced groove between distal medial and lateral condyles, robust corpus calcanei, upper molars mesostyles strong and with concave labial wall of metacone, metaconid-entoconid generally not fused lingually to form a circle on p4; Table 1), but also with the other anoas (e.g., humerus with squared top corner of distal medial condyle, ectostylids are generally present only in m1, p2 is absent, vertical groove between protoconid and hypoconid on p4 is V-shaped; Table 1). An expanded top of distal medial condyle of the humerus, the presence of a straight parastylid in m3 and of an entostylid not fused with entoconid in p4 are not observed in the living anoas and may be autapomorphies for the new species (Table 1).

Age and distribution: The species is likely Late Pleistocene/Holocene in age, based on the geology of the region, stratigraphic, archaeological and biochronological evidence, and absolute datings (see Aubert et al., 2014; Van den Bergh et al., 2016). The species is known from several localities in South Sulawesi (see below).

Etymology: The specific epithet is a noun in the genitive singular case, honoring professor Colin Peter Groves (Australian National University) for his singular and inspiring contribution to the taxonomy of anoas.

Description and comparison

Humerus: only parts of the distal epiphysis and diaphysis are preserved in the right humerus RGM.1317484 from Pangareang Tudea (levels C-D), south coast of South Sulawesi. The specimen is slightly larger than those of *B. depressicornis* and *B. quarlesi*, while it is smaller than those of *B. cebuensis* and *B. mindorensis*, as evidenced by the available humeral measurements (Fig. 3; Table 2). The top corner of the distal medial condyle is squared as in the living anoas and in *B. arnee*, while it is roughly rounded in *B. cebuensis* and *B. mindorensis*. The top of the distal medial condyle has a peculiar outline, that markedly expands towards the diaphysis; this profile is cut away in all the other insular buffaloes and in *B. arnee*. As in *B. cebuensis* and *B. arnee*, a well-defined and pronounced groove between the distal medial and lateral condyles is present in *B. grovesi*; the groove is shallow and less developed in *B. depressicornis*, *B. quarlesi* and *B. mindorensis*. Unfortunately, the incomplete specimen does not allow to verify the shape of the deltopectoral crest, the size of the greater tuberosity, and other diagnostic features of the proximal epiphysis of the humerus (see Croft et al., 2006).

To investigate size and shape variation of the humerus in *Bubalus*, a bivariate plot, including the available humeral measurements of *B. grovesi*, was built (Fig. 5). The position of the specimen NN in the plot highlights the peculiar size of *B. grovesi* with respect to the other insular buffaloes and suggests that the new species is characterised by a relatively wider distal articular surface of the humerus.

Metacarpal: three incomplete right metacarpals (RGM.1317469, RGM.1317470, RGM.1317471) from Leang Tomatoa Kacicang in the Lamoncong area, all missing the distal epiphysis and part of the diaphysis, are referred to the new species (Figs. 2, 4). As in the case of the humerus, available linear measurements and the respective scatter plot show that these specimens are slightly larger

than the metacarpals of *B. depressicornis* and *B. quarlesi* (Fig. 5, Table 2). An estimate of metacarpal length for *B. grovesi* would suggest an animal roughly similar in stature to *B. mindorensis*; in contrast, the breadth of this bone would suggest a less massive animal. A medial prominence on the magnum-trapezoid facet is absent in the new species as well as in both *B. depressicornis* and *B. mindorensis*, while it is present in *B. quarlesi* and *B. arnee*. A pronounced tubercle on the medial side of the proximal epiphysis seems to characterise all the living insular buffaloes, but not *B. grovesi*. Accordingly, the medial side of the magnum-trapezoid facet appears rather flattened in the new species, although this may be an artifact of preservation. As in the other anoas and in *B. mindorensis*, the uncinatus facet does not protrude posteriorly and its palmar side is cut away. Unfortunately, it was impossible to make comparisons with *B. cebuensis*, since no metacarpals of the fossil buffalo from the Philippines have been recovered thus far (see Croft et al., 2006).

Astragalus: one complete right astragalus (RGM.1317485) of *B. grovesi* comes from the older levels (C-D) of Pangareang Tudea cave, south coast of South Sulawesi. The specimen is smaller than those of *B. mindorensis*, but it is larger than the available one of *B. quarlesi* and than most of those of *B. depressicornis*, although it falls within the variation range of dimensions of the extant lowland species (Figs. 4, 5; Table 2). The morphology of the astragalus of *B. grovesi* is similar to that of other *Bubalus*. The most conspicuous feature is the presence of a prominence above the distal condyles in dorsal view. This closely resembles the condition seen in some individuals of *B. quarlesi*, while no prominences can be observed in *B. mindorensis*, *B. depressicornis*, and *B. arnee*. As in the case of metacarpals, no comparative specimens of *B. cebuensis* were available (see Croft et al., 2006).

A small and damaged astragalus, retrieved from the upper levels (A-B) of Pangareang Tudea cave, could either belong to a juvenile individual of *B. grovesi* or to an adult individual of *B. quarlesi* (see Hooijer, 1950). Unfortunately, the preservation status of the specimen does not allow to recognise any diagnostic feature.

Calcaneum: an incomplete right calcaneum (RGM.1317486), coming from the older levels (C-D) of Pangareang Tudea cave and lacking the distal extremity, is assigned to the new species. The length of the corpus from the processus cochlearis and the greatest width over the sustentaculum show that the specimen is similar in size to the larger ones of *B. depressicornis*, while it is larger than the available calcaneum of *B. quarlesi* and smaller than those of *B. mindorensis* (Table 2). In the new species, the corpus calcanei is robust as in *B. mindorensis* and *B. arnee*, while it is more gracile in *B. depressicornis* and *B. quarlesi*. The shape of the capus in proximal view is rounded; conversely, it is rather pointed and angular in all the other insular buffaloes. Unfortunately, it was impossible to make comparisons with *B. cebuensis*, since no comparative specimens were available (see Croft et al., 2006).

Metatarsal: the distal epiphysis of a metatarsal (RGM.1317487) of *B. grovesi* was recovered from Pangareang Tudea (levels C-D). It is clearly a metatarsal, and not a metacarpal, as shown by the extension of the median dorsal groove down to the distal sagittal notch. The specimen is slightly larger than the metatarsals of *B. quarlesi* and *B. depressicornis* (it falls just outside of the variation range of dimensions of the extant lowland species), while it is smaller than those of *B. cebuensis* and *B. mindorensis*, as evidenced by the available linear measurements and the respective scatter plot (Figs. 4, 5; Table 2). The most conspicuous feature of the metatarsal in dorsal view, the sulcus for the extensor digitorum longus tendon, is not broad as in *B. cebuensis*, while it is equal in width to those of *B. mindorensis* and *B. depressicornis*. However, as in the case of *B. cebuensis*, the sulcus differs from those of *B. mindorensis*, *B. quarlesi*, *B. depressicornis* and *B. arnee* in lacking overarching sides, although this may be an artifact of preservation (Fig. 4; Table 1).

Phalanges: one intermediate phalanx (RGM.1317488) of *B. grovesi* comes from the older levels (C-D) of Pangareang Tudea, while one proximal phalanx (RGM.1317479), one intermediate phalanx (RGM.1317480), and one distal phalanx (RGM.1317481) were retrieved from the younger levels (A-B) of the same cave. Available linear measurements show that these specimens are similar in size to the phalanges of *B. depressicornis*, while they are smaller than those of *B. mindorensis* and

B. cebuensis (Table 1). Although the morphology of the phalanges of *B. grovesi* is similar to that of other *Bubalus*, some minor differences can be recognised.

For instance, the proximal phalanx of the new species is characterised by a proximal articular surface that expands towards the extensor tubercles, as in *B. depressicornis* and *B. arnee*, while it is not or less expanded in *B. mindorensis*. Furthermore, a strong intake is present above the distal articular end in medial/lateral view and a marked tubercle is developed on the palmar/plantar side of the shaft; a less pronounced tubercle is also present in the same position in a few specimens of *B. depressicornis* (e.g., USNM 219297), while it is absent in *B. mindorensis* and *B. arnee*.

The two intermediate phalanges from Pangareang Tudea show very different dorsal-ventral dimensions of the medial and lateral portions of the proximal articular facet, as in *B. arnee* and *B. mindorensis*; conversely, in *B. depressicornis* the two portions of the proximal articular surface are more similar in size. Furthermore, the proximal articular surface markedly projects from the palmar/plantar side in the new species; this feature seems to be shared by *B. mindorensis*, while it is not observed in *B. depressicornis* and in *B. arnee*.

The most conspicuous feature of the distal phalanx of *B. grovesi* is the absence of a large, antero-posteriorly elongate depression on the postero-lateral surface, that, instead, characterises other buffaloes, such as *B. depressicornis*, *B. cebuensis*, and some individuals of *B. arnee*. On the other hand, the presence of one or more large nutrient foramina in the same position more closely resembles the condition observed in *B. mindorensis*. Unfortunately, it was impossible to make comparisons with *B. quarlesi*, since no phalanges were available.

Morphological variation and the absence of articulated specimens of the new species prevented me from assessing whether the focal elements represent manual or pedal phalanges. However, measurements of articulated bovid specimens suggest that, while forelimb and hindlimb phalanges can differ in absolute size within an individual, their proportions are relatively constant (Degusta and Vrba, 2005). Accordingly, a principal component analysis was performed to explore size and shape variation in the phalanges among different insular buffaloes (Fig. 6). Seven, seven, and five

measurements, listed in Fig. 6, were used in the analyses of proximal, intermediate, and distal phalanges, respectively (for a complete description of the measurements see Degusta and Vrba, 2005). While those measurements have been mainly used to infer habitat preference in previous studies (e.g., Degusta and Vrba, 2005; Rozzi and Palombo, 2013; Rozzi et al., 2013), they are also valuable in investigating differences in proportions and in providing some additional insight into the taxonomy of the new species. The factor loadings for the first 2 principal components (PCs) are shown in Table 3 and the specimens are plotted against these two factors in Fig. 6. As expected, PC1 clearly represents size, since all variables have high positive loadings and the variable affecting the first component the most is the maximal length of each bone, which accounts from more than 65% of the distal phalanges to more than 53% of the proximal phalanges (see Table 3).

Accordingly, in all the graphs, *B. grovesi* plots closer to *B. depressicornis* on the first axis than to any other species. Furthermore, the only available specimen of *B. cebuensis*, a distal phalanx, is positioned between the anoas and *B. mindorensis* (see Fig. 6). The occurrence of the largest species - *B. mindorensis* - at the peripheric area of each plot highlights once more the increasing body size trend along the first component axis (capturing more than 90% of the variance in all the phalanges). PC2 represents robustness in the analysis of proximal phalanges; proximal, intermediate and distal diameters (WP, WI, WD) have high positive loadings, while midline length (LM) has a high negative loading. Accordingly, this axis clearly distinguishes the relatively robust proximal phalanges of *B. depressicornis* and *B. mindorensis* from the more gracile proximal phalanx of *B. grovesi*.

A similar scenario characterises the principal component analysis of the intermediate phalanges. Again, PC2 represents robustness; proximal and distal diameters (WP, WD) show high positive loadings, and inferior and superior lengths (LI, LS) show negative loadings. This axis clearly separates the stout intermediate phalanges of *B. depressicornis* from the more slender intermediate phalanx of *B. grovesi*, while the robustness of the specimen of *B. mindorensis* is intermediate between these two taxa.

The dispersion of distal phalanges along the second component axis is mainly related to differences in the basal width (WB), inferior length (LI), and total height (HT), for which I obtained the highest positive values in the PCA loadings (see Table 3). Accordingly, the robustness of the proximal end plays a key role in the distribution of the focal specimens: the more gracile distal phalanges of *B. depressicornis* and *B. cebuensis* are clearly separated from the one of *B. grovesi*, characterised by a relatively wider proximal articular surface; the position of the specimen of *B. mindorensis* is intermediate between these two groups.

All in all, the position of the phalanges of *B. grovesi* in the PCA score plots - well separated with respect to those of the other insular buffaloes - highlights their peculiar biometry and morphology.

Premolars: in addition to one p4, included in a dental series from Sompe, Sopeng district, one left P3/P4 (RGM.1317472) and one right p4 (RGM.1317473) from Leang Tomatoa Kacicang, in the Lamoncong area, are referred to the new species (Fig. 4). Available linear measurements show that the specimens are slightly larger than the premolars of *B. quarlesi* - they fall just inside the size range of *B. depressicornis* -, while they are smaller than those of *B. mindorensis* (Table 2). In overall form, they closely resemble the corresponding teeth of other anoas, although some significant features can be recognised in the p4. The metaconid and the entoconid are not fused in the posterior lower premolar of *B. grovesi*, as in *B. mindorensis* and *B. arnee*, while they are fused lingually to form a circle in *B. depressicornis* and *B. quarlesi*. Another feature that the new species shares with the extant representatives of the subgenus *Bubalus* is the presence of a deep anterior transverse valley on the internal side of p4. This valley is rather shallow in the other anoas. The presence of a well-separated entostylid and entoconid characterises the p4 of *B. grovesi*; conversely, those elements are fused together in all the other living insular buffaloes and in *B. arnee*. A well-separated entostylid and entoconid can also be observed in one specimen retrieved from Bola Batu (RGM.1317511, Van Heekeren collection), but additional evidence is needed in order to delve into the intraspecific variation of this feature and to confirm the occurrence of the new species in the deposits of that cave. In fact, according to Hooijer (1950), all the remains from Bola Batu would

belong to *B. quarlesi*. Unfortunately, no comparisons with *B. cebuensis* were possible, since no premolars of the fossil buffalo from Cebu Island have been recovered thus far (see Croft et al., 2006).

Molars: in addition to the ones that form the dental series from Sompe, Sopeng district, several upper and lower molars of *B. grovesi* come from the Toalian caves of Pangareang Tudea (levels A-B and C-D) and Leang Tomatoa Kacicang. Scanty specimens were also retrieved along the Walanae river valley at Ciangkange, south of the Cabenge-Pampanua road, Beru, and Celeko (Fig. 4). Both upper and lower molars of *B. grovesi* are slightly larger than the ones of fossil/subfossil and extant *B. quarlesi* - they fall just inside of the variation range of dimensions of *B. depressicornis* -, while they are smaller than those of *B. cebuensis* and *B. mindorensis*, as evidenced by the available linear measurements and the respective bivariate plots (Fig. 7; Table 2). In particular, the scatter plots of M1/M2, M3 and m1/m2 highlight the peculiar dimensions of the molars of *B. grovesi*, that form a rather distinct and compact group with respect to the other fossil/subfossil specimens of anoa. Scanty molars of anoa were also retrieved from Batu Ejaya 1, south coast of South Sulawesi, and Panisi Takbutu, Bone area, but they are too incomplete to be studied and measured. Accordingly, the occurrence of *B. grovesi* in the latter sites cannot be confirmed.

Although the morphology of the molars of *B. grovesi* is similar to that of the other anoa, a few significant differences can be recognised. Upper molars mesostyles are strong and with concave labial wall of metacone behind as in *B. mindorensis* and *B. arnee*, while they are less developed in the other anoa. The parastylid of m3 has a peculiar straight shape, while it is curved in all the other extant insular buffaloes and in *B. arnee*. Another conspicuous feature of the posterior lower molar is the presence of a pointed metastylid. This closely resembles the condition seen in some individuals of *B. depressicornis*, while a more rounded metastylid can be observed in *B. mindorensis*, *B. quarlesi* and *B. arnee*. Comparisons were also made with m1-2 of *B. cebuensis* and the diagnostic differences in the general dental morphology of *Bubalus* and *Anoa* were recognised (e.g., the presence/absence of ectostylids; see revised diagnosis above).

4. Fossil and subfossil *Anoa*: how many species?

The classification of the living anoas into two species is accepted by the majority of the specialists, although a number of studies have suggested that the taxonomic diversity of anoas could have been underestimated (see, e.g., Sugiri and Hidayat, 1996; Kikkawa et al., 1997; Burton et al., 2005; Groves and Grubb, 2011). For instance, Hooijer (1950) stated that Van Bemmelen considered *B. quarlesi* to have valid geographic races, but no new name or description has been proposed (see Groves, 1969). A similar scenario characterises the fossil and subfossil remains of anoa, too. A few authors have shown evidence of the coexistence of large and small anoas in the Sulawesi Subrecent to Recent Faunas and have hinted to the existence of distinct subspecies (see e.g., Sarasin, 1905; Hooijer, 1948, 1950). In particular, Hooijer (1950) recognised that rather large anoa bones and teeth occurred in some Toalian caves and that one tooth from Leang Tomatoa Kacancang was even above the limits found for *B. depressicornis*. However, no new species were described in the past 65 years, mainly due to the absence of detailed information about morphological features of insular buffaloes and the lack of specimens for comparison.

On the basis of an accurate review of the material studied by Hooijer, and of the postcranial and dental features exhibited by living and extinct dwarfed buffaloes, here I described a new species of *Bubalus* (*Anoa*) from the Late Pleistocene/Holocene of South Sulawesi. Accordingly, the largest remains of fossil and subfossil anoa, ascribed to *B. depressicornis* by Hooijer (1950) mainly on the basis of differences in size, were assigned to the new species. The coexistence of *B. grovesi* with the smaller *B. quarlesi* was confirmed only in one site, the Toalian cave Pangareang Tudea in the south coast of South Sulawesi. Relatively small postcranial remains, collected at Leang Tomatoa Kacancang and ascribed by Hooijer (1950) to *B. quarlesi*, exhibit a combination of features that is not in agreement with the former attribution and, pending further investigation, are provisionally listed here as Bovidae indet. A few deciduous teeth in the sample from Pangareang Tudea were not

ascribed to the new species, since no significant differences in size and morphology were observed with respect to the subfossil deciduous teeth of *B. quarlesi* retrieved from Bola Batu (see Hooijer, 1950).

All in all, results obtained suggest that two species of anoa occurred in the Subrecent Fauna of Sulawesi: *B. quarlesi* and *B. grovesi*. Accordingly, the evolution and first occurrence of the lowland anoa, *B. depressicornis*, on the island would be more recent than previously assumed (see below).

5. Body size and insular dwarfing

In previous studies, linear dimensions of teeth have been used to ascertain the size differences between extant and fossil/subfossil anoas (Sarasin, 1905; Dammerman, 1939; Hooijer, 1948, 1950). However, tooth size cannot be confidently used for endemic dwarfed mammals because in several cases they have relatively larger teeth with respect to the body size than their full-sized ancestors (see e.g., Gould, 1975; Fortelius, 1985; Lister, 1989; Köhler and Moyà-Solà, 2004). In fact, size reduction in insular dwarfs is not generally isometric across all parts of the body. Furthermore, as already stressed by Hooijer (1950), differences in size between the anoas are “average” rather than absolute and variation ranges of dental and postcranial dimensions partially overlap.

Accordingly, to delve into the size differences between *B. grovesi* and the other dwarfed buffaloes, I estimated their body masses. Average mass estimates obtained for the species in the study are shown in Fig. 8. This comprehensive overview of body masses of dwarfed buffaloes, based on specimens stored in several American and European museums (see above and Appendix A), is extremely valuable. In fact, accurate body masses of rare ungulates are very difficult to obtain since this type of information is rarely recorded in the field, and body mass estimates listed for these mammals frequently include only trophy or zoo animals (which are not representative of the species in general) and many juvenile individuals. Conversely, only adult individuals and several specimens captured in the wild were included in the database of this study (see Appendix A). Results obtained

indicate a reasonable mass estimate of 117 kg for the new species, *B. grovesi*. Given the variability in estimates derived from individual measurements in living taxa, this estimate is probably within 15% of the true mass of this fossil animal (Scott, 1983). My estimates for *B. depressicornis* and *B. quarlesi* suggest that the data published thus far would slightly overestimate the body mass of these species (see e.g., Burton et al., 2005; Croft et al., 2006). Accordingly, the discrepancy in reported adult weights of the living anoas (body masses of *B. depressicornis* and *B. quarlesi* are <300 and <150 kg, respectively, according to Burton et al., 2005; average body mass of *B. depressicornis* is 135 kg according to Croft et al., 2006) is possibly due to the scantiness of published data and/or to the inclusion of zoo and/or misidentified specimens in the measured samples. Results obtained indicate that *B. grovesi* was about 30% larger than *B. depressicornis* and 50% larger than *B. quarlesi*, making it the largest representative of the subgenus *Anoa* reported thus far. The new species was about 25% smaller than the fossil buffalo from Cebu Island, *B. cebuensis*, and its body mass was about half the one of *B. mindorensis*. Although inferred metacarpal length suggest a stature similar to that of *B. mindorensis*, body mass estimates paint a picture of a slender animal. Furthermore, morphological features (e.g., the breadth of the dorsal longitudinal sulcus of the metatarsal) and available measurements of long bones epiphyses (e.g., humerus, metacarpal, metatarsal) support this reconstruction (see description).

One of the most recurring patterns in insular vertebrates is the island rule, describing a graded trend from gigantism in small species to dwarfism in large species. Rozzi and Palombo (2014) showed that body size trends of insular extant and fossil bovids are in agreement with the island rule pattern and that island bovids would have reduced their body size in relation to a variety of forces (e.g., characteristics of the islands and the species itself and release from ecological pressures of competition and predation). In order to explore the size shift of the new species and the other dwarfed buffaloes in light of the island rule, I calculated their body size divergence S_i (see Materials and Methodology). The estimate rests on the assumption that fossil water buffaloes (see below and Dong et al., 2014) would be the ancestors of the anoas, *B. cebuensis*, and *B. mindorensis*,

and that the body masses of those putative ancestors would not differ significantly from that of their extant relative *B. arnee*. The relative size of *B. grovesi* (body size divergence, S_i) indicates an average body size reduction of about 89% ($S_i = 0.11$) with respect to a typical water buffalo. *Bubalus depressicornis* and *B. quarlesi* exhibit even more extreme values, with a body size reduction of about 92% ($S_i = 0.08$) and 93% ($S_i = 0.07$), respectively. Endemic buffaloes from the Philippines are more massive than the anoas and their relative size indicates an average body size reduction of about 79% ($S_i = 0.21$) for *B. mindorensis* and of about 85% ($S_i = 0.15$) for *B. cebuensis*.

Given its peculiar morphological features and its smaller size with respect to a typical water buffalo, it is clear that *B. grovesi* represents another case of insular dwarfing. The complexity of causal mechanisms behind the island rule is highlighted by the presence on different islands (e.g., *B. mindorensis* and *B. depressicornis*) and even on the same island (*B. grovesi*, *B. depressicornis* and *B. quarlesi*) of species showing different body size reductions even if originating from ancestors of similar size. Accordingly, in order to delve into the tempo and mode of the island dwarfing experienced by *B. grovesi* and, more in general, by the anoas, it is imperative to gather evidence coming from different disciplines and use it to discuss the origin and evolution of the subgenus.

6. Phylogenetic relationships and biogeography: a multidisciplinary perspective

The taxonomy and biogeography of the anoas have been sources of confusion ever since the first specimens were described (Burton et al., 2005 and references therein). In particular, uncertainty remains over their phylogenetic relationships, timing of colonization, and mode of evolution. Here, I integrate new evidence on the taxonomy and body size reduction of the anoas with available data from different disciplines in order to provide insights into the origin and evolution of the subgenus. Fossil and subfossil remains of two species of anoa, *B. quarlesi* and *B. grovesi*, have been found in the Sulawesi Subrecent to Recent Faunas of Late Pleistocene to Holocene age (Van den Bergh et

al., 2001), but not from earlier deposits as suggested previously (Hooijer, 1950). In fact, no remains of those taxa have yet been found in situ in the Tanrung Formation (Middle/Late Pleistocene) and materials of historical collections, collected along the Walanae river valley, would likely come from Late Pleistocene or younger unconsolidated colluvial/alluvial deposits (see Van den Bergh, 1999; Van den Bergh et al., 2001). This claim is supported by the discovery of a lower molar fragment of *Bubalus* sp., slightly above the size range for *B. depressicornis*, from Late Pleistocene deposits at Talepu, a newly excavated site in the Walanae Basin (the molar fragment would be $>103 \pm 9$ kyr and $<126 \pm 11$ kyr in age on the basis of infrared stimulated luminescence dating of sediment samples; see Van den Bergh et al., 2016). All in all, *Bubalus grovesi* would have occurred on Sulawesi since the Late Pleistocene, while absolute dates and culture history of Toalian cave sites suggest an early Holocene first occurrence for *B. quarlesi* (see Table 4 for a chronology of selected localities). Additional evidence of the presence of the subgenus *Anoa* in the region during the Late Pleistocene is provided by large naturalistic paintings in local prehistoric art sites in the Maros karst and in the Bone region (see Fig. 9). According to Aubert et al. (2014), two broad periods in the Maros-Pangkep rock art production can be recognised and the earliest of those is characterised by human hand stencils and large naturalistic paintings of endemic Sulawesian mammals, such as the anoa, the babirusa, and the Celebes warty pig. Recently, uranium-series dating of speleothems associated with prehistoric art from seven sites in the Maros area revealed ages between 35000 and 40000 years BP (see Aubert et al., 2014 for a detailed chronology). Other paintings, discovered at Gua Batti, a cave in the regency of Bone, include a large depiction of anoa (Fig. 9) and they are stylistically identical to the ones in Maros. Accordingly, a similar age can be inferred for them, although they could not be dated because of the absence of speleothems (Aubert et al., 2014; Tacon et al., 2014; Tan, 2014). Another painting of anoa, similar in style and, probably, in age to the one in the Gua Batti cave, characterises the spectacular gallery of Sumpang Bitu, in Pangkep regency (Fig. 9; Bulbeck, 2004 and references therein).

Several morphological studies of extant anoa skulls suggested that *Anoa* diverged about 2 Mya from the ancestral *Proamphibos*–*Hemibos* lineage leading to the living Asiatic buffaloes (Pilgrim, 1939; Groves, 1969, 1981; Burton et al. 2005). New evidence in this study - such as the presence in the representatives of the subgenus *Anoa* of apomorphic features resulting from the evolution under insular conditions (see above) - does not support that scenario. Furthermore, a close affinity with the Asian water buffalo is confirmed and a more recent divergence, directly from a representative of the genus *Bubalus*, is suggested for *Anoa*. The putative ancestor of *B. grovesi*, the most archaic species of the anoa lineage, presumably reached Sulawesi during the Middle/Late Pleistocene and experienced a relatively rapid evolution in a carnivore-free environment, including a significant body size reduction and a marked shortening of metapodials (see Rozzi and Palombo, 2014 for a discussion about the evolutionary patterns of insular bovids). This scenario is also supported by regional sea-level oscillations and by the palaeogeographic history of the area. During the Pleistocene, the Sunda Islands, were frequently connected with each other and with the Southeast Asian mainland. During glacial phases, the sea level dropped between about 40 and 120 m, resulting in the exposure of the Sunda Shelf (Voris, 2000; Meijaard, 2004). As already hinted by Van den Bergh et al. (2001), it is probable that the ancestors of the taxa recognised in the Subrecent to Recent Faunas of Sulawesi reached the island during periods of low sea level, when sea barriers must have been less extensive than the present-day ones. For instance, the width of the Makassar Strait, that separates South Sulawesi from the east coast of Borneo, may have been reduced to a minimum of about 50 km during glacial phases (Van den Bergh et al., 2001). Furthermore, several shallow carbonate platforms south of the Makassar Basin may have also served as stepping stone islands and may have provided occasional dispersal routes. In agreement with the taxonomic evidence presented in the study, the most reasonable ancestor of the anoa would be *Bubalus palaeokerabau*, occurring on Java since the Early/Middle Pleistocene (Van den Bergh et al., 2001), or *Bubalus arnee*, occurring on Java, Sumatra, and possibly on other Sunda Islands, since the Late Pleistocene (cf. Punung and Lida Ajer faunas; Tougaard, 2001; Van den Bergh et al., 2001).

However, the hypothesis of a colonization from Borneo through the Makassar Strait cannot be excluded on the basis of the palaeogeographic evolution of the area, although it is not supported by palaeontological evidence. In fact, no fossil remains of water buffalo have been found on Borneo thus far and the only bovid recorded in the Late Pleistocene and Holocene of the island is the banteng, *Bos javanicus* (Cranbrook, 2010). A dispersal of the ancestor of the anoa from the Lesser Sunda Islands seems very unlikely because of their isolated position with respect to Sulawesi and because no bovid remains have been retrieved from pre-Holocene deposits on those islands (Meijer et al., 2010; Van der Geer et al., 2010). A colonization via the China-Taiwan-Philippine route was already excluded by Van den Bergh et al. (2011).

A number of theories have been advanced to explain the presence of two extant morphologically similar species of anoa on Sulawesi. These include separate immigrations, environmental variation resulting from altitude, forest fragmentation, vicariance, and radiation (see Burton et al., 2005 and references therein). At first glance, new morphological and palaeontological evidence, including a body size reduction trend, with the largest anoa specimens found in the older sites and the smallest ones in the younger sites, would seem to support a single lineage model. However, the co-occurrence of *B. grovesi* and *B. quarlesi* at Pangareang Tudea contradicts, at least partially, such a scenario. Accordingly, a single colonization - radiation model seems more substantiated: *B. grovesi* and *B. quarlesi* would have originated from an ancestral stock during a supposedly long-standing isolation. *Bubalus depressicornis*, virtually absent in the Subrecent Fauna of Sulawesi, would have evolved from *B. grovesi* only in the late Holocene. The virtual demise of *B. grovesi* by the middle to late Holocene is also confirmed by the heavy reduction in the number of anoa remains recovered from the corresponding levels at several lowland Toalian sites (e.g., Maros karst, Pangareang Tudea; Simons and Bulbeck, 2004).

Several genetic studies have been conducted to investigate the evolution and systematics of *Anoa* (Burton et al. 2005, and references therein). Different results have been obtained, although most of those studies support the two living species taxonomic status. On the one hand, some authors

suggested that the anoas might be members of a plesiomorphic clade of Bovini and supported the placing of *Anoa* as a subgenus within *Bubalus* and the hypothesis that the endemic subgenus diverged from the ancestral bovine lineage about 2 Mya (Savage and Russell, 1983; Hartl et al., 1988; Schreiber et al., 1990; Kakoi et al., 1994; Tanaka et al., 1996). On the other hand, a few studies proposed older divergence times for *Anoa* (e.g., 12.4 Mya according to Pitra et al., 1997; 4,3 Mya according to Stelbrink et al., 2012) and suggested a close phylogenetic relationship with the genus *Boselaphus* (Pitra et al., 1997). Recent phylogenetic studies of Bovini, based on analyses of mitochondrial sequences and multiple nuclear genes, obtained an Early Pleistocene divergence time for the genus *Bubalus* (1.29 ± 0.48 Mya; Hassanin et al., 2012, 2013) that would suggest an even more recent divergence time for the endemic *Anoa*. Unfortunately, most of genetic studies did not take into account information about the fossil record and the morphology of *Anoa*, and about the palaeogeographic history and sea level shifts across the Sundaic province, especially during the Quaternary. Here, I adopted a multidisciplinary approach and I summarised and discussed information from different fields to better understand the complicated evolutionary history of the subgenus. Accordingly, three alternative palaeobiogeographic scenarios can be inferred by integrating available evidence (Fig. 10):

- 1) Early divergence from Bovini (about 12.4 Mya) and close phylogenetic proximity with *Boselaphus*

This hypothesis, based on results of nuclear DNA analyses (Pitra et al., 1997), is not supported by the fossil record of Sulawesi and by morphological evidence. Conversely, results obtained in this study confirm a close relationship between *Anoa* and *Bubalus* and do not support the putative plesiomorphic status of the main features exhibited by the focal subgenus (see above). Furthermore, the palaeogeographic history of the area is not in agreement with an early immigration, since Sulawesi was still very far from the Sundaic land mass during the Middle Miocene.

2) Late divergence (about 4-2 Mya) from the ancestral *Proamphibos-Hemibos* lineage

This model is supported by genetic studies (see Burton et al. 2005 and references therein; Stelbrink et al., 2012) and classic morphological studies (e.g., Pilgrim, 1939; Groves, 1969). However, results obtained here are not in agreement with a divergence from the ancestral Siwaliks taxa. Furthermore, no fossil/subfossil remains of anoa have yet been found in the Middle Pleistocene deposits of Sulawesi (cf. Tanrunga Formation; see Van den Bergh et al., 2001) and, according to palaeogeographic reconstructions, the Makassar Strait was still too wide to provide occasional dispersal routes for the ancestor of *Anoa* during the Late Pliocene/Early Pleistocene.

3) Recent divergence (Middle/Late Pleistocene) from *Bubalus*

New morphological evidence suggests a recent divergence for *Anoa*, directly from a representative of the genus *Bubalus*. Results of recent genetic studies (see Hassanin et al., 2012, 2013 and above), the fossil record and prehistoric art of Sulawesi and the other Sunda Islands are in agreement with this scenario. Additional support comes from palaeogeographic data and reconstructions of regional sea-level shifts (Voris, 2000; Meijaard, 2004; Sathiamurthy and Voris, 2006; Hall, 2013; Larick and Ciochon, 2015) that suggest a minimum distance between South Sulawesi and the Sundaic land mass during Middle/Late Pleistocene glacial phases.

All in all, the latter hypothesis, according to which the representatives of the subgenus *Anoa* may be dwarfed forms of the Asian water buffalo that arose following dispersal to Sulawesi, seems to be the most substantiated. Given the contrasting results of genetic studies and the rarity of fossils of anoa, details of such a scenario remain provisional. However, available evidence from different disciplines supports this general interpretation.

7. Conclusion

Although our knowledge on the endemic buffaloes from Sulawesi is limited by small sample sizes, results obtained here provide important data on the origin and evolution of the subgenus *Anoa*. Fossil and subfossil remains of two species of anoa occurred in the Late Pleistocene/Holocene deposits of Sulawesi: *B. quarlesi* and a new species, formally named here *B. grovesi*. The lowland anoa, *B. depressicornis*, evolved on the island more recently than previously assumed. *Bubalus grovesi* sp. nov. should be considered as the most archaic and the largest representative of the subgenus. Its ancestor presumably reached Sulawesi during the Middle/Late Pleistocene and experienced a relatively rapid body size reduction and shortening of metapodials under insular conditions. Finally, results obtained stress the usefulness of a multidisciplinary approach in investigating the phylogenetic relationships and biogeography of fossil and living taxa.

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References

Aubert, M., Brumm, A., Ramli, M., Sutikna, T., Saptomo, E.W., Hakim, B., Morwood, M.J., Van den Bergh, G.D., Kinsley, L., Dosseto, A., 2014. Pleistocene cave art from Sulawesi, Indonesia. *Nature*. 514, 223-227.

Bartstra, G.J., 1977. Walanae formation and Walanae terraces in the stratigraphy of south Sulawesi (Celebes, Indonesia). *Quartär*. 27, 21-30.

Bartstra, G.J., 1997. A fifty years commemoration: fossil vertebrates and stone tools in the Walanae valley, South Sulawesi, Indonesia. *Quartär*. 47, 29-50.

Bohlken, H., 1958. Vergleichende untersuchungen an wildridern (Tribus Bovini Simpson, 1945). *Zool. Jahr*. 68, 113–220.

Bulbeck, D., Pasqua, M., Di Lello, A., 2000. Culture history of the Toalean of south Sulawesi, Indonesia. *Asian Perspect*. 39, 71-108.

Bulbeck, F., 2000. A historical perspective on the Australian contribution to the practice of archaeology in Southeast Asia. *Austral. Archaeol.* 50, 45-53.

Bulbeck, F., 2004. Divided in space, united in time: The Holocene prehistory of South Sulawesi. In: Keates, S.G., Pasveer, J.M. (Eds.), *Modern Quaternary Research in Indonesia* 18. A A Balkema, The Netherlands, pp. 129-166.

Burton, J.A., Hedges, S., Mustari, A.H., 2005. The taxonomic status, distribution and conservation of the lowland anoa *Bubalus depressicornis* and mountain anoa *Bubalus quarlesi*. *Mamm. Rev.* 35, 25–50.

Cannon, C.H., Summers, M., Harting, J.R., Kessler, P.J.A., 2007. Developing conservation priorities based on forest type, condition, and threats in a poorly known ecoregion: Sulawesi, Indonesia. *Biotropica*. 39, 747-759.

Clason, A.T., 1976. A preliminary note about the animal remains from the Leafing I Cave, South Sulawesi, Indonesia. *MQRISA*. 2, 53-67.

Clason, A.T., 1980. Mesolithic hunter-gatherers in Sulawesi. *BIPPA*. 2, 65-68.

Clason, A.T., 1987. Late Pleistocene/Holocene hunter-gatherers of Sulawesi. *Palaeohistoria*. 29, 67-76.

Clough, Y., Abrahamczyk, S., Adams, M.O., Anshary, A., Ariyanti, N., Betz, L., Buchori, D., Cicuzza, D., Darras, K., Putra, D.D., Fiala, B., 2010. Biodiversity patterns and trophic interactions in human-dominated tropical landscapes in Sulawesi (Indonesia): plants, arthropods and vertebrates.

In: Tscharrntke T., et al. (Eds.), Tropical Rainforests and Agroforests under Global Change. Springer Science and Business Media, Berlin Heidelberg, pp. 15-71.

Corbet, G.B., Hill, J.E., 1992. The Mammals of the Indomalayan Region: A Systematic Review. Natural History Museum Publications and Oxford University Press, Oxford, UK.

Cranbrook, E.O., 2010. Late quaternary turnover of mammals in Borneo: the zooarchaeological record. *Biodivers. Conserv.* 19, 373-391.

Croft, D.A., Heaney, L.R., Flynn, J.J., Bautista, A.P., 2006. Fossil remains of a new, diminutive *Bubalus* (Artiodactyla: Bovidae: Bovini) from Cebu Island, Philippines. *Journ. Mamm.* 87, 1037-1051.

Dammerman, K.W., 1939. On prehistoric mammals from South Celebes. *Treubia.* 17, 63-72.

DeGusta, D., Vrba, E., 2005. Methods for inferring paleohabitats from the functional morphology of bovid phalanges. *J. Achaeol. Sci.* 32, 1099–113.

Dolan, J.M., 1965. Breeding of the lowland anoa, *Bubalus (Anoa) d. depressicornis* (H. Smith, 1927) in the San Diego Zoological Garden. *Zeits. fur Sauget.* 30, 241–248.

Dong, W., Liu, J.Y., Zhang, L.M., Xu, Q.Q., 2014. The Early Pleistocene water buffalo associated with *Gigantopithecus* from Chongzuo in southern China. *Quat. Int.* 354, 86-93.

Fortelius, M., 1985. Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. *Acta Zool. Fenn.* 108, 1–76.

Gentry, A.W., 1992. The subfamilies and tribes of the family Bovidae. *Mamm. Rev.* 22, 1–32.

Glover, I.C., 1981. Leafing Burung 2: an upper palaeolithic rock shelter in south Sulawesi, Indonesia. *MQRSA*. 6, 1-38.

Gould, S.J., 1975. On the scaling of tooth size in mammals. *Am. Zool.* 15, 351–362.

Groves, C.P., 1969. Systematics of the anoa (Mammalia, Bovidae). *Beaufortia*. 17, 1–12.

Groves, C.P., 1980. Notes on the systematics of *Babyrousa* (Artiodactyla, Suidae). *Zool. Med.* 55, 29-46.

Groves, C.P., 1981. Systematic relationships in the bovini (Artiodactyla, Bovidae). *J. Zoolog. Syst. Evol. Res.* 19, 264-278.

Groves, C.P., Grubb, P., 2011. *Ungulate Taxonomy*. Johns Hopkins University Press, Baltimore.

Hall, R., 2013. The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *J. Limnol.* 72, 1-17.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeont. Electr.* 4, 1–9.

Hartl, G., Göltenboth, R., Grillitsch, M., Wiliing, R., 1988. On the biochemical systematics of the Bovini. *Biochem. Sys. Ecol.* 16, 575–579.

Hassanin, A., Delsuc, F., Ropiquet, A., Hammer, C., Jansen van Vuuren, B., Matthee, C., Ruiz-Garcia, M., Catzeflis, F., Areskoug, V., Nguyen, T.T., Couloux, A., 2012. Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. *C. R. Biol.* 335, 32–50.

Hassanin, A., Ropiquet, A., Nguyen, T.T., Couloux, A., 2013. Combining multiple autosomal introns for studying shallow phylogeny and taxonomy of Laurasiatherian mammals: Application to the tribe Bovini (Cetartiodactyla, Bovidae). *Mol. Phylogenet. Evol.* 66, 766-775.

Hooijer, D.A., 1948. Pleistocene vertebrates from Celebes. III. *Anoa depressicornis* (Smith) subsp., and *Babyrousa babirussa beruensis* nov. subsp. *Proc. kon. Ned. Akad. Wetensch.* 51, 1322-1330.

Hooijer, D.A., 1950. Man and other mammals from Toalian sites in Southwestern Celebes. *Verh. kon. Ned. Akad. Wetensch. Afd. Natuurk.* 46, 1-164.

Hooijer, D.A., 1972. Pleistocene vertebrates from Celebes: XIV. Additions to the *Archidiskodon-Celebochoerus* fauna. *Zool. Med.* 46, 1-16.

Janis, C.M., 1990. Correlation of cranial and dental variables with body size in ungulates and macropodoids. In: Damuth J., MacFadden B.J. (Eds.), *Body Size in Mammalian Paleobiology: Estimations and Biological Implication*. Cambridge University Press, Cambridge, pp. 255–300.

- Kakoi, H., Namikawa, T., Takenaka, O., Takenaka, A., Amano, T., Martojo, H., 1994. Divergence between the anoas of Sulawesi and the asiatic water buffaloes, inferred from their complete amino acid sequences of hemoglobin b chains. *Z. Zool. Syst. Evolut.* 32, 1–10.
- Kappelman, J., Plummer, T., Bishop, L., Appleton, A.D., Appleton, S., 1997. Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. *J. Hum. Evol.* 32, 229–256.
- Kikkawa, Y., Yonekawa, H., Suzuki, H., Amano, T., 1997. Analysis of genetic diversity of domestic water buffaloes and anoas based on variations in the mitochondrial gene for cytochrome b. *Anim. Genet.* 56, 21–24.
- Köhler, M., Moyà-Solà, S., 2004. Reduction of brain and sense organs in the fossil insular bovid *Myotragus*. *BBE.* 63, 125–139.
- Larick, R., Ciochon, R.L., 2015. Early hominin biogeography in Island Southeast Asia. *Evol. Anthropol. Issues News Rev.* 24, 185–213.
- Lister, A.M., 1989. Rapid dwarfing of red deer on Jersey in the last interglacial. *Nature.* 342, 539–542.
- Lomolino, M.V., 2005. Body size evolution in insular vertebrates: generality of the island rule. *J. Biogeogr.* 32, 1683–1699.
- Lomolino, M.V., Van der Geer, A.A.E., Lyras, G.A., Palombo, M.R., Sax, D.F., Rozzi, R., 2013. Of mice and mammoths: generality and antiquity of the island rule. *J. Biogeogr.* 40, 1427–1439.

- Martinez, J.-N., Sudre, J., 1995. The astragalus of Paleogene artiodactyls: comparative morphology, variability and prediction of body mass. *Lethaia* 28, 197–209.
- Meijaard, E., 2004. Solving mammalian riddles: A reconstruction of the Tertiary and Quaternary distribution of mammals and their palaeoenvironments in island South-East Asia. PhD Thesis. School of Archaeology and Anthropology, The Australian National University, Canberra, Australia.
- Meijer, H.J., Van den Hoek Ostende, L.W., Van den Bergh, G.D., De Vos, J., 2010. The fellowship of the hobbit: the fauna surrounding *Homo floresiensis*. *J. Biogeogr.* 37, 995-1006.
- Mohr, E., 1921. Die geographische verbreitung der anoa-arten auf Celebes. *Arch. Natur.* 87, 208–214.
- Nowak, R.M., 1997. Walker's Mammals of the World. 6th ed. Johns Hopkins University Press, Baltimore, Maryland.
- Ouwens, P.A., 1910. Contribution a la connaissance des mammiferes de Celebes. *Bull. Dept. Agric. Indes Néerl.* 38, 1-7.
- Palombo, M.R., Köhler, M., Moyà-Solà, S., Giovinazzo, C., 2008. Brain versus body mass in endemic ruminant artiodactyls: a case studied of *Myotragus balearicus* and smallest *Candiacervus* species from Mediterranean Islands. *Quat. Int.* 182, 160-183.
- Pilgrim, G.E., 1939. The fossil Bovidae of India. *Mem. Geol. Surv. India.* 26, 1–356.

- Pitra, C., Furbass, R., Seyfert, H.M., 1997. Molecular phylogeny of the tribe Bovini (Mammalia: Artiodactyla): alternative placement of the Anoa. *J. Evol. Biol.* 10, 589–600.
- Plagnes, V., Causse, C., Fontugne, M., Valladas, H., Chazine, J.M., Fage, L.H., 2003. Cross dating (Th/U-¹⁴C) of calcite covering prehistoric paintings in Borneo. *Quat. Res.* 60, 172–79.
- Rozzi, R., 2010. I bovidi endemici del Pleistocene inferiore della Sardegna: plesiomorfie ed apomorfie nello scheletro postcraniale. MS Thesis. Sapienza, Università di Roma, Rome, Italy.
- Rozzi, R., 2014. Palaeobiogeography and evolution of insular bovids: ecogeographic patterns of body mass variation and morphological changes. PhD Thesis, Sapienza, Università di Roma, Rome, Italy.
- Rozzi, R., Winkler, D.E., De Vos, J., Schulz, E., Palombo, M.R., 2013. The enigmatic bovid *Duboisia santeng* (Dubois, 1891) from the Early-Middle Pleistocene of Java: a multiproxy approach to its palaeoecology. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 377, 73-85.
- Rozzi, R., Palombo, M.R., 2013. Do methods for predicting palaeohabitats apply for mountain and insular fossil bovids? *Integr. Zool.* 8, 244-259.
- Rozzi, R., Palombo, M.R., 2014. Lights and shadows in the evolutionary patterns of insular bovids. *Integr. Zool.* 9, 213-228.
- Sarasin, F., 1905. Die Tierreste der Toála-Höhlen. In: Sarasin, P., Sarasin, F. (Eds.), *Materialien zur Naturgeschichte der Insel Celebes*, pp. 29-55.

- Sathiamurthy, E.V.H.K., Voris, H.K., 2006. Maps of Holocene sea level transgression and submerged lakes on the Sunda Shelf. *Nat. Hist. J. Chulalongkorn Univ.* 2, 1-43.
- Savage, D.E., Russell, D.E., 1983. *Mammalian Paleofaunas of the World*. Addison-Wesley, Reading, MA.
- Schreiber, A., Goltenboth, R., 1990. The haemoglobins of wild cattle (Bovini Simpson, 1945). *Z. Säugetierkd.* 55, 276–283.
- Schreiber, A., Nötzold, G., 1995. One EEP, but how many anoas? In: Rietkerk, F., et al. (Eds.), *EEP Yearbook 1994/95*. EAZA/EEP Executive Office, Amsterdam, the Netherlands, pp. 419-424.
- Schreiber, A., Seibold, I., Nötzold, G., Wink, M., 1999. Cytochrome b gene haplotypes characterize chromosomal lineages of anoa, the Sulawesi dwarf buffalo (Bovidae: *Bubalus* sp.). *J. Hered.* 90, 165–76.
- Scott, K.M., 1983. Prediction of body weight of fossil Artiodactyla. *Zool. J. Linn. Soc.* 77, 199-216.
- Scott, K.M., 1990. Postcranial dimension of ungulates as predictors of body mass. In: Damuth J., MacFadden B.J. (Eds.), *Body Size in Mammalian Paleobiology: Estimations and Biological Implication*. Cambridge University Press, Cambridge, pp. 301–336.
- Semiadi, G., Mannullang, B., Burton, J., Schreiber, A., Mustari, A.H., and the IUCN SSC Asian Wild Cattle Specialist Group, 2008a. *Bubalus depressicornis*. The IUCN Red List of Threatened Species 2008: e.T3126A9611738. Downloaded on 10 September 2015.

Semiadi, G., Burton, J., Schreiber, A., Mustari, A.H., 2008b. *Bubalus quarlesi*. The IUCN Red List of Threatened Species 2008: e.T3128A9613851. Downloaded on 10 September 2015.

Simons, A., Bulbeck, D., 2004. Late Quaternary faunal successions in South Sulawesi, Indonesia. In: Keates S.G., Pasveer J.M. (Eds.), Modern Quaternary Research in Indonesia 18, A A Balkema, The Netherlands, pp. 167-190.

Stelbrink, B., Albrecht, C., Hall, R., von Rintelen, T., 2012. The biogeography of Sulawesi revisited: is there evidence for a vicariant origin of taxa on Wallace's "anomalous island"? Evolution. 66, 2252-2271.

Sugiri, N., Hidayat, N., 1996. The diversity and hematology of anoa from Sulawesi. In: Manansang, J., et al. (Eds.), Population and Habitat Viability Assessment Workshop for the Anoa (*Bubalus depressicornis* and *Bubalus quarlesi*) Report. Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley, MN, pp. 138-151.

Taçon, P.S., Tan, N.H., O'Connor, S., Xueping, J., Gang, L., Curnoe, D., Bulbeck, D., Hakim, B., Sumantri, I., Than, H., Sokrithy, I., 2014. The global implications of the early surviving rock art of greater Southeast Asia. Antiquity. 88, 1050-1064.

Tan, N.H., 2014. Rock Art Research in Southeast Asia: A Synthesis. Arts. 3, 73-104.

Tanaka, T., Solis, C.D., Masangkay, J.S., Maeda, K., Kawamoto, Y., Namikawa, T., 1996. Phylogenetic relationship among all living species of the genus *Bubalus* based on DNA sequences of cytochrome b gene. Biochem. Genet. 34, 443-452.

- Tougard, C., 2001. Biogeography and migration routes of large mammal faunas in South–East Asia during the Late Middle Pleistocene: focus on the fossil and extant faunas from Thailand. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 168, 337-358.
- UNEP-WCMC, 2011. UNEP-WCMC species database: CITES-listed species. UNEP-WCMC.
- Van den Bergh, G.D., 1999. The Late Neogene elephantoid-bearing faunas of Indonesia and their palaeozoogeographic implications. *Scripta Geol.* 117, 1-419.
- Van den Bergh, G.D., De Vos, J., Sondaar, P.Y., 2001. The Late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 171, 385-408.
- Van den Bergh, G.D., Li, B., Brumm, A., Grün, R., Yurnaldi, D., Moore, M.W., Kurniawan, I., Setiawan, R., Aziz, F., Roberts, R.G., Storey, M., 2016. Earliest hominin occupation of Sulawesi, Indonesia. *Nature* 529, 208-211.
- Van der Geer, A.E.E., Lyras, G., De Vos, J., Dermitzakis, M., 2010. *Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands*. Wiley–Blackwell, Oxford.
- Van Heekeren, H.R., 1972. *The Stone Age of Indonesia*. Martinus Nijhoff, The Hague.
- Voris, H.K., 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *J. Biogeogr.* 27, 1153-1167.

Weise, R., 1979. Untersuchungen zur innerartlichen variabilität beim anoa (*Anoa depressicornis*).
Staatsexamenarbeit, Universität Kiel, Germany.

Whitten, A.J., Mustafa, M., Henderson, G.S., 1987. The Ecology of Sulawesi. Gadjah Mada
University Press, Yogyakarta, Indonesia.

Whitten, A.J., Mustafa, M., Henderson, G.S., 2002. The ecology of Sulawesi. Periplus, Singapore.

Wilson, D.E., Reeder, D.M., 1993. Mammal Species of the World: A Taxonomic and Geographic
Reference. Smithsonian Institution Press, Washington, USA and London, UK.

Captions

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).

Fig. 2. Selection of right metacarpals of dwarfed buffaloes. From left to right: *Bubalus grovesi* from Leang Tomatoa Kacicang, Lamoncong area, Sulawesi (RGM.1317470); *Bubalus quarlesi* from Toratja, Sulawesi (ANSP 19186); *Bubalus depressicornis* from Sulawesi (FMNH 98791); *Bubalus mindorensis* from Lumanta River, Mindoro, The Philippines (FMNH 219049).

Fig. 3. Selection of right humeri of dwarfed buffaloes. From left to right: *Bubalus grovesi* from Pangareang Tudea (levels C-D), south coast of South Sulawesi (RGM.1317484); *Bubalus quarlesi* from Toratja, Sulawesi (ANSP 19186); *Bubalus depressicornis* from Sulawesi (USNM 219297); *Bubalus mindorensis* from Mindoro, The Philippines (FMNH 18817); *Bubalus cebuensis* from Cebu, The Philippines (FMNH PM 61097).

Fig. 4. Selection of postcranial and dental remains of *Bubalus grovesi*: one partial metatarsal (RGM.1317487) in dorsal view (a); one partial right calcaneum (RGM.1317486) in plantar (b1) and lateral (b2) view; one right astragalus (RGM.1317485) in plantar (c1) and dorsal (c2) view; one proximal phalanx (RGM.1317479) in dorsal (d1) and axial (d2) view; one intermediate phalanx (RGM.1317480) in dorsal (e1) and axial (e2) view; one distal phalanx (RGM.1317481) in axial (f1) and dorsal (f2) view; one partial right metacarpal (RGM.1317471) in proximal (g1) and dorsal (g2) view; one partial right metacarpal (RGM.1317469) in proximal (h1) and dorsal (h2) view; one

dental series (p4-m3; RGM.1317497) in buccal view; one M1/M2 (RGM.1317467) in buccal (j1) and occlusal (j2) view; one m1/m2 (RGM.1317495) in lingual (k1) and occlusal (k2) view; one m3 (RGM.1317496) in lingual (l1) and occlusal (l2) view; one m3 (RGM.1317483) in lingual (m1) and occlusal (m2) view; one M1/M2 (RGM.1317491) in buccal (n1) and occlusal (n2) view; one M1/M2 (RGM.1317489) in buccal (o1) and occlusal (o2) view; one p4 (RGM.1317473) in buccal (p1) and occlusal (p2) view; one M1/M2 (RGM.1317475) in buccal (q1) and occlusal (q2) view; one M3 (RGM.1317476) in buccal (r1) and occlusal (r2) view. For a complete list of the specimens in the study see Appendix A.

Fig. 5. Bivariate plots of linear measurements for humerus, metacarpal, astragalus, and metatarsal for selected specimens of dwarfed buffaloes in the study. For abbreviations of measurements see Appendix B.

Fig. 6. Results of the PCA analysis for phalanges of dwarfed buffaloes in the study. Abbreviations of measurements, following DeGusta and Vrba (2005).

Fig. 7. Bivariate plots of linear measurements for M1/M2, M3, m1/m2, and m3 for selected specimens of dwarfed buffaloes in the study. For abbreviations of measurements see Appendix B.

Fig. 8. Body mass estimates of selected living and extinct representatives of *Bubalus* (*Bubalus*) and *Bubalus* (*Anoa*). The dagger symbol (†) is used to designate extinct species. The scheme shows the buffaloes in the study in proportion to a 1.8 meter tall human.

Fig. 9. Prehistoric paintings of anoa from Gua Batti, Bone regency (on the left), and Sumpang Bitu, Pangkep regency (on the right). Courtesy of Maxime Aubert and Luc-Henri Fage, respectively.

Fig. 10. Three alternative palaeobiogeographic scenarios describing the origin and evolution of *Anoa*: 1) Early divergence from Bovini (about 12.4 Mya) and close phylogenetic proximity with *Boselaphus*; 2) Late divergence (about 4-2 Mya) from the ancestral *Proamphibos-Hemibos* lineage; 3) Recent divergence (Middle/Late Pleistocene) from *Bubalus*. Check and x marks indicate available data from different disciplines that support or do not support each model. Maps modified from Meijaard (2004).

Tab. 1. Variation in selected morphological characters among species of *Bubalus*. Character states shared between *B. grovesi* and other species are underlined; character states that are autapomorphic for *B. grovesi* are italicized.

Tab. 2. Factor loadings and proportion of variation for first 2 principal components (PCs) from principal component analyses of *Bubalus* proximal, intermediate, and distal phalanges. PC1 accounts for about 93.9%, 96.1%, and 90.5% of the variation in the respective datasets; PC2 accounts for about 4.24%, 3.42%, and 7.2%, respectively.

Tab. 3. Postcranial and dental measurements (mm) for the dwarfed buffaloes in the study. All the species are represented by sample statistics (mean (sample size) range). For abbreviations of measurements see Fig. 6 and Appendix B.

Tab. 4. Estimated age of selected sites and biochronological range of the representatives of the subgenus *Anoa*.

Table

	Morphological character	<i>B. grovesi</i>	<i>B. depressicornis</i>	<i>B. quarlesi</i>	<i>B. mindorensis</i>	<i>B. cebuensis</i>
Humerus	Top of distal medial condyle	<i>expanded</i>	cut away	cut away	cut away	cut away
	Top corner of distal medial condyle	<u>squared</u>	<u>squared</u>	<u>squared</u>	rounded	rounded
	Groove between distal medial and lateral condyles	<u>pronounced</u>	slight	slight	slight	<u>pronounced</u>
Metacarpal	Metacarpal with or without a medial prominence on magnum-trapezoid facet	<u>without</u>	<u>without</u>	with	<u>without</u>	?
Metatarsal	Sides of the dorsal longitudinal sulcus	<u>not overarching</u>	slightly overarching	strongly overarching	strongly overarching	<u>not overarching</u>
Calcaneus	Corpus calcanei	<u>robust</u>	gracile	gracile	<u>robust</u>	?
	Shape of the capus in proximal view	rounded	angular	angular	angular	?
Astragalus	Prominences above the distal condyls in dorsal view	<u>single</u>	absent	<u>single</u>	absent	?
Distal phalanx	Large, anteroposteriorly elongate depression on the posterolateral surface	<u>absent</u>	present	?	<u>absent</u>	present
Upper molars	Upper molars mesostyles strong and with concave labial wall of metacone behind	<u>strong</u>	weak	weak	<u>strong</u>	?
p2		<u>absent</u>	<u>absent</u>	<u>absent</u>	present	?
p4	Vertical groove between protoconid and hypoconid	<u>V shaped</u>	<u>V shaped</u>	<u>V shaped</u>	U shaped	?
	p4 with shallow or deep anterior transverse valley on the internal side	<u>deep</u>	shallow	shallow	<u>deep</u>	?
	Metaconid-entoconid generally not fused or fused lingually to form a circle on p4	<u>not fused</u>	fused	fused	<u>not fused</u>	?
	Entostylid present or fused with entoconid	<i>present</i>	fused	fused	fused	?
Lower molars	Ectostylids (basal pillar) on all lower molars (0), lost in m2-m3 (1), lost in m1-m3 (2)	<u>lost in m2-m3</u>	<u>lost in m2-m3</u>	<u>lost in m2-m3</u>	on all lower molars	?
m3	Parastylid	<i>straight</i>	curved	curved	curved	?
	Metastylid	<u>pointed</u>	<u>pointed</u>	rounded	rounded	?

Table

	Measur ement	<i>B. grovesi</i>	<i>B. quarlesi</i> (fossil/subfos sil)	<i>B. quarlesi</i> (extant)	<i>B.</i> <i>depressicorn</i> <i>is</i>	<i>B.</i> <i>mindorensis</i>	<i>B.</i> <i>cebuensis</i>
Humerus	DTAD	47, 05 (1)		37,1 (1)	40,53 (6) 36,02-42,73	59,02 (2) 57,52-60,52	50,21 (2) 48,7-51,72
	DTTD	49,04 (1)		48,74 (1)	49,03 (6) 40,82-52,25	70,1 (2) 66,6- 73,6	56,25 (2) 56,06-56,43
Metacarpal	PTD	36,02 (3) 35,43-37,08		31,27 (1)	32,96 (6) 28,61-35-47	50,34 (2) 47,25-53,43	
	PAPD	21,74 (3) 21,02-22,22		18,09 (1)	18,13 (6) 15,79-19,34	28,09 (2) 27,68-28,49	
Metatarsal	DTD	34,3 (1)		32,47 (1)	32,21 (4) 29,13-33,66	49,48 (2) 49,14-49,81	42,06 (1)
	DAPD	18,59 (1)		17,56 (1)	18,2 (4) 17,2- 18,76	25,56 (2) 25,28-25,84	23,77 (1)
Astragalus	L	41,15 (1)	37 (1)	37,07 (1)	39,09 (5) 36,06-42,17	58,08 (2) 58- 58,15	
	I	25,3 (1)	21 (1)	22,12 (1)	23,65 (5) 19,75-25,37	34,06 (2) 33,82-34,3	
Calcaneum	LC	62,9 (1)		63,27 (1)	59,55 (2) 59- 60,09	86,08 (2) 80,12-92,03	
	SW	25,42 (1)		26,22 (1)	23,95 (2) 23,73-24,16	41,86 (2) 40,98-42,73	
Proximal phalanx	WP	16,25 (1)			17,21 (4) 16,71-17-89	26,35 (1)	
	WI	14,98 (1)			15,57 (4) 15,15-16,04	24,1 (1)	
	WD	15,36 (1)			17,19 (4) 16,29-18,04	24,4 (1)	
	LM	41,72 (1)			38,62 (4) 36,06-40,77	50,14 (1)	
	HI	14,43 (1)			14,94 (4) 13,69-16,04	20,57 (1)	
	HD	10,74 (1)			12,32 (4) 12- 12,76	17,9 (1)	
	HP	16,18 (1)			16,05 (4) 15,1-17,4	21,2 (1)	
Intermediate phalanx	WP	16,77 (2) 15,96-17,57			17,23 (2) 16,2-18,25	26,6 (1)	
	WD	11,91 (2) 11,46-12,36			13,47 (2) 12,58-14,35	21,08 (1)	
	LS	28,82 (2) 27,94-29,69			26,34 (2) 25,54-27,14	42,09 (1)	
	LI	29,5 (2) 28,46-30,53			25,06 (2) 24,52-25,59	41,96 (1)	
	HD	13,25 (2) 12,97-13,53			12,51 (2) 11,41-13,6	18,26 (1)	
	HL	12,9 (2) 12,79-13,01			10,91 (2) 10,16-11,66	16,95 (1)	
	HM	16,78 (2) 16,27-17,29			14,54 (2) 14,01-15,06	20,75 (1)	
Distal phalanx	LS	29,51 (1)			35,94 (2) 31,85-40,03	48,11 (1)	44,11 (2) 43,4-44,82
	LI	32,72 (1)			30,18 (2) 26,98-33,37	52,56 (1)	39,31 (2) 38,4-40,21
	WB	15,85 (1)			12,29 (2)	20,95 (1)	16,83 (2)

					11,44-13,14		16,5-17,15
	HT	30,35 (1)			25,64 (2) 21,48-29,8	40,15 (1)	34,62 (2) 34,53-34,7
	HA	14,39 (1)			13 (2) 12,38- 13,62	15 (1)	15,2 (2) 14,21-16,19
P3/P4	L	11, 68 (1)	10,05 (11) 9,06-11,14	9,76 (8) 7,56- 10,82	11,85 (19) 9,46-14,19	13,2 (8) 10,62-15,03	
	W	9,98 (1)	8,87 (11) 7,11-11,84	8,51 (8) 6,34- 10,39	10,68 (19) 8,03-13,13	12,94 (8) 10,1-16,21	
p4	L	13,77 (2) 13,5-14,03	12,32 (3) 11,94-12,98	11,25 (3) 10,47-12,2	12,88 (4) 10,27-15,46	15,69 (5) 14,92-16,13	
	W	7,84 (1)	6,26 (3) 5,97- 6,44	5,78 (3) 4,34- 6,66	7,27 (4) 4,56- 9,38	9,49 (5) 8,8- 9,92	
M1/M2	L	17,51 (8) 16,25-19,4	15,01 (18) 12- 17,16	14,88 (8) 10,97-16,18	16,47 (20) 12,13-19,64	19,44 (16) 16,32-22,6	
	W	14 (8) 11,73- 16,6	10,27 (18) 7,71-13	12,32 (8) 11,15-13,42	14,09 (20) 11,16-15,8	18,22 (14) 15,76-19,33	
M3	L	21,19 (2) 21- 21,37	15 (9) 13,4- 16,53	15,83 (4) 14,57-17,47	18,51 (11) 15,08-21,11	21,38 (8) 19,57-24,06	
	W	15,1 (2) 14,8- 15,4	10,54 (9) 8- 11,98	11,39 (4) 9,2- 13,28	13,8 (11) 11,01-16,15	17,51 (7) 14,84-18,77	
m1/m2	L	17,74 (5) 17,03-18,4	15,37 (14) 13,11-16,75	14,27 (10) 11,24-16,17	16,38 (14) 11,81-21,14	19,35 (14) 16,12-23,03	17,38 (2) 16,55-18,2
	W	9,07 (5) 8,31- 9,9	7,44 (14) 6,35-8,04	8,51 (10) 7,98-9,52	9,31 (14) 7,74-11,44	12 (12) 11,13- 13,36	11,58 (2) 10,95-12,21
m3	L	22,19 (3) 20,61-25	20,23 (7) 18,6-22,84	20,08 (7) 18,14-22,44	22,37 (7) 18,09-26,03	28,19 (6) 27- 29,7	
	W	8,33 (2) 7,74- 8,91	7,77 (7) 7,24- 8,9	8,64 (7) 6,72- 10,3	9,45 (7) 7,51- 11,03	11,33 (5) 10,62-11,85	

Table

Proximal phalanx			Intermediate phalanx			Distal phalanx		
Variables	PC1	PC2	Variables	PC1	PC2	Variables	PC1	PC2
LM	0,5357	-0,7486	LS	0,5597	-0,0207	LS	0,5249	-0,8316
WP	0,4415	0,2658	LI	0,5802	-0,4549	LI	0,667	0,3255
WI	0,4071	0,2266	WP	0,3588	0,4677	HA	0,06725	0,06907
WD	0,3595	0,4321	WD	0,3031	0,6578	HT	0,4687	0,2883
HP	0,2546	-0,1222	HL	0,2053	-0,2249	WB	0,2352	0,3384
HI	0,2835	-0,08714	HM	0,2098	-0,2915			
HD	0,2792	0,3292	HD	0,2082	0,07504			
Variation explained (%)	93,856	4,2353	Variation explained (%)	96,08	3,4174	Variation explained (%)	90,508	7,1907

Table

Site	Sumpang Bitu	Gua Battil	Leang Burung 2	Sompe	Beru	Ciangkange	Celeko	Lagosi	Pangareang Tudea	Leang Pattae	Bola Batu	Batu Ejaya 1	Leang Tomatoa Kacang
Age	Late Pleistocene	Late Pleistocene; about 35000-40000 BP	Late Pleistocene; 31260±320 BP (layers II-XI) or older (layer I)	Late Pleistocene-Holocene	Late Pleistocene-Holocene	Late Pleistocene-Holocene	Late Pleistocene-Holocene	Late Pleistocene-Holocene	early Holocene (levels C-D); middle to late Holocene (levels A-B)	Holocene	Holocene	middle to late Holocene	middle Holocene to about 2000 BP
<i>Bubalus grovesi</i>				X	X	X	X		X				X
<i>Bubalus quarlesi</i>									X		X	X	
<i>Bubalus</i> sp.			X					X		X			
Prehistoric art	X	X											
References	Bulbeck et al., 2000	Bulbeck et al., 2000	Glover, 1981; Simons & Bulbeck, 2004	Van den Bergh, 1999	Van den Bergh, 1999	Van den Bergh, 1999	Van den Bergh, 1999	Van den Bergh, 1999	Van Heekeren 1972; Glover, 1976; Bulbeck, 2004; Simons & Bulbeck, 2004	Bulbeck, 2000, 2004; Simons & Bulbeck, 2004	Bulbeck et al., 1987; Simons & Bulbeck, 2004	Hooijer, 1950; Bulbeck, 2000, 2004; Simons & Bulbeck, 2004	Bulbeck et al., 1987; Simons & Bulbeck, 2004

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