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## Systematics of the Anoa (Mammalia, Bovidae)

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### ABSTRACT

The systematic position of the Anoa is discussed, with reference to its nomenclature and taxonomic history. Two distinct types of Anoa are found all over Celebes, a large one with white legs, long tail and rugged horns, and a small one with legs mainly the same colour as the body, short tail and conical horns. There is some indication that the small Anoa inhabits mountainous areas. In the absence of any evidence of intergradation they must be classed as two distinct species; since the Anoa is closely related to the Indian Buffalo and the Tamarao, the two must be called *Bubalus (Anoa) depressicornis* and *B. (A.) quarlesi*.

The Anoa is the Dwarf Buffalo of Celebes. While closely similar to the Asiatic Buffalo (*Bubalus*), many authors (Mohr, 1921; Pilgrim, 1939; Hooijer, 1948, 1950) have regarded the Anoa as forming a genus on its own, *Anoa* H. Smith, 1827. Others (Dolan, 1965) have regarded it as a subgenus within the genus *Bubalus*; yet others (Bohlken, 1958) have not regarded *Anoa* as valid even subgenerically.

The Anoa shows similarity to the Asiatic Buffaloes of genus *Bubalus* in several very cogent characters, as follows: the section of the horn-cores is triangular, with a sharp inner keel; the palate is thickened and firmly united to the vomer; the frontal is highly convex; the hair tends to become sparse in adults, and on the midline of the neck is directed cranial; the hoofs are broad; the body is stout and rounded, and the back nearly straight, with little of the elongation of the thoracic neural spines which is characteristic of the related genera (subgenera) *Bos*, *Bibos* and *Bison*. The genus most closely allied to *Bubalus* and the Anoa is that for the African Buffaloes, *Syncerus*; this latter, however, differs in lacking two of the strongest specialisations (vomer-palate fusion, and reversal of nuchal hairstream), and has a marked specialisation of its own, the tendency of the horn-bases to expand and meet across the midline of the forehead.

The definitive fusion of vomer to palatines is a long-established character; according to Pilgrim (1939) it was shown already in the Dhok Pathan (Plio-

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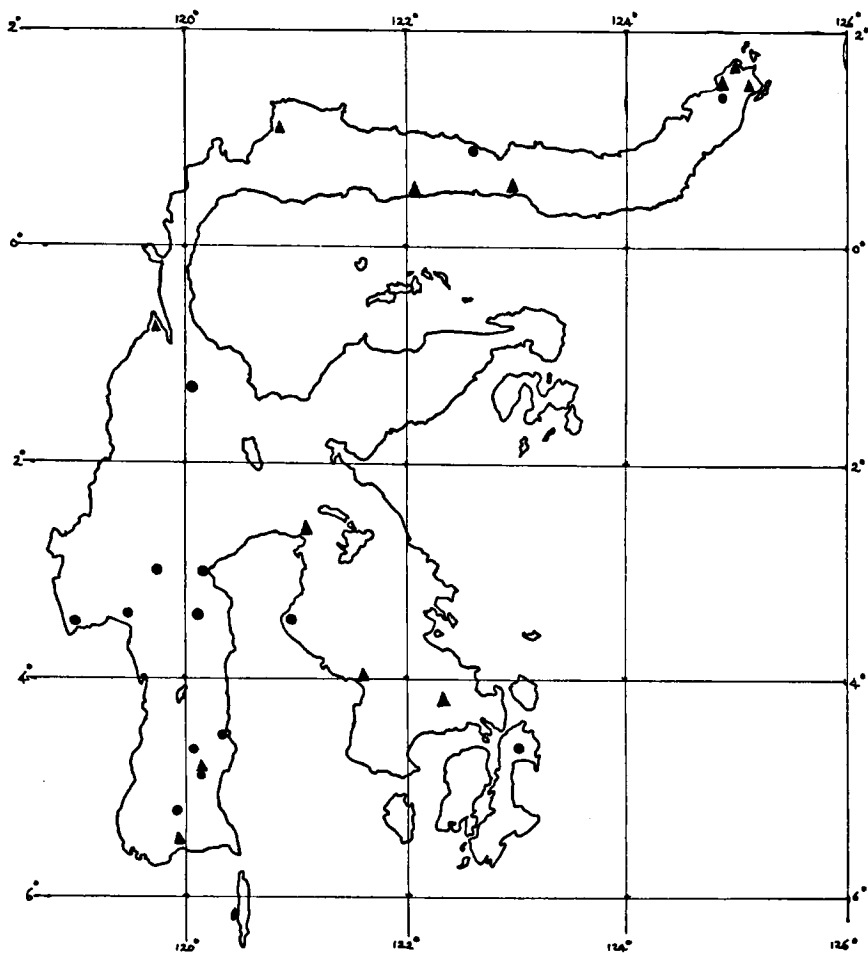


FIG. 1. Distribution of subgenus *Anoa*, in historical times (see distribution records in text) if not today.

Key: ▲ *Bubalus (Anoa) depressicornis*

● *Bubalus (Anoa) quarlesi*

Note that the only two records of *B. (A.) depressicornis* from the southwestern peninsula are from Toalian living sites (Hooijer, 1950), not present-day.

cene) genus *Proamphibos*. Consequently the generic separation of *Bubalus* from *Syncerus* seems thoroughly justified, and some at least of the similarity between them (such as that in the shape of the horn-cores) must be put down to parallelism.

The position of the *Anoa*, whether it should actually be classified within the genus *Bubalus*, is not so easy to decide. It has, as shown by Pilgrim (1939), some features in common with the Villafranchian ancestral genus *Hemibos*, and even with *Proamphibos*: the horn-cores are small, not curved and only slightly divergent; the parietal is less reduced than in *Bubalus* and

inclined at more of an angle to the occipital, less to the frontal; the occipital is higher, narrower; the orbits are less prominent. It may be remarked, however, that these differences are relatively minor, and that the similarity between an Anoa and a young Indian Buffalo is very striking in the skull and externally.

Three tooth characters are given by various authors to differentiate the Anoa from *Bubalus*: In the Anoa, there are accessory columns only on  $M_1$ , not on  $M_{2-3}$ ; the protoconid of  $P_4$  is gradually convex from before backward instead of having a median outer rib marked off posteriorly, so that the protoconid-hypoconid groove is V-shaped, less broad; and the anterior transverse valley on the internal side of  $P_4$  is blocked.

With regard to the first character, Heller as long ago as 1889 showed that the accessory columns may occur on all three lower molars in some Anoa. In the second character, Hooijer (1948), who first discovered the difference, commented himself that the median outer rib may be hardly developed in some *Bubalus*, so that the difference may be almost invisible. In the third case, too, the difference is not absolute: the closure of the anterior valley may be more or less expressed, and in B.M. 607b is not seen at all.

The conclusion is, that the Anoa shows all the specialised characters of *Bubalus* and few cogent or absolute differences; generic allocation to *Bubalus* is therefore advocated. Within *Bubalus* proper, two species may be recognised, and equally within the Anoa (as shown later in this paper); so that *Anoa* H. Smith, 1827, is best employed as a subgenus to indicate these relationships.

When one compares Anoa from all over Celebes, one finds constantly two forms: a large one with triangular, flattened and wrinkled horn, and a small one with conical horns which are rounded in section. The juvenile stages of the large form closely resemble the adult of the small form; but at all stages the large form has the forelegs, from the knees to the hoofs, white, except for a black line down the front and another crossing this at rightangles over the fetlocks; and the hindlegs have conspicuous white spots above the hoofs. These markings are yellow in the infant, and become clearer and whiter with age; they are well shown in photographs in Dolan (1965), and are never present in the small form. The small form also has a shorter tail than the large one; except for this difference and the matter of the colouration, the small form is essentially a paedomorphic variety of the large one.

The two forms are found all over Celebes, but wherever locality records are available, either in the literature or on labels of specimens seen in the present study, the small form is found in mountainous country, the large one in the lowlands. In some cases, however, the same locality is given as having both species (such as Menado; also the "caves north of Tjani" (Hooijer, 1950) for fossil Anoa); moreover there is no specimen seen by the present author that cannot at once be referred to its species, and there are no intermediates. Accordingly, until such time as evidence may be discovered that they intergrade at a certain altitude, the two will be maintained as separate species.

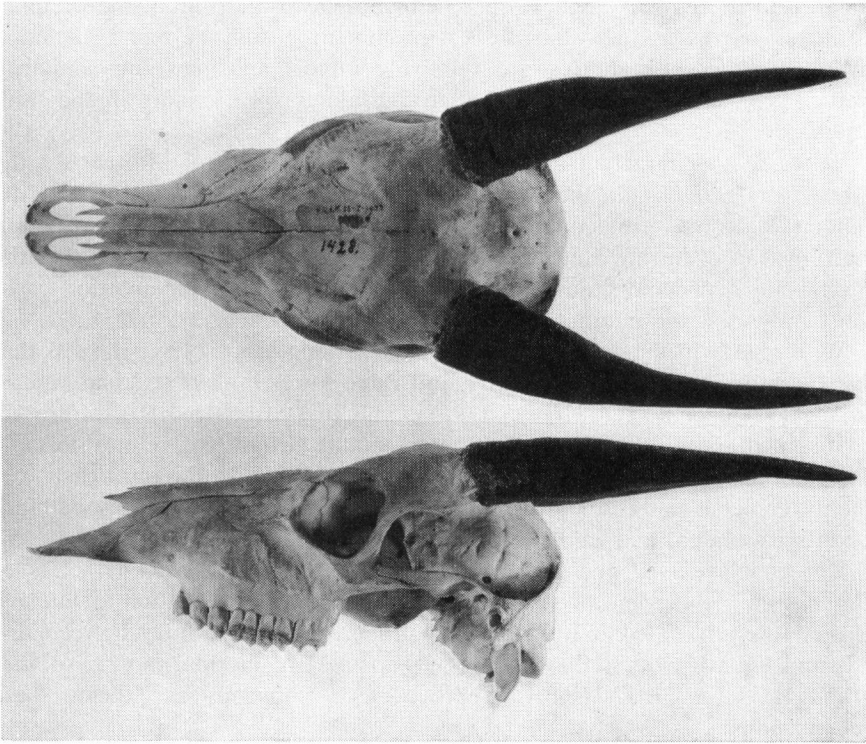


FIG. 2. *Bubalus (Anoa) depressicornis* H. Smith, 1827: young adult male skull from Donggala, ZMA 1428. Skull length 296 mm; horn length 195 mm (unusually small for this species). Notice the flattening of the basal half of the horns, the wrinkling, and the marked expansion of the external angle.

The first scientific description of an Anoa was by Hamilton Smith (1827), who named it *Antelope depressicornis*, erecting at the same time the subgenus *Anoa* for it. The description, as well as the holotype itself, a nearly complete skull with horns in the British Museum (Natural History), leave no doubt that the form being described is the large species. The later names *Oreas platyceros* Temminck, 1853, and *Probubalus celebensis* Rütimeyer, 1865, are essentially substitute names for *depressicornis*.

The first name given to Anoa which was not intended as a substitute was Lydekker's (1905) *Bos depressicornis fergusonii*. The description of this new subspecies is a little confused; in one place Lydekker says that the type specimen is a young Anoa, "in the thick woolly coat of youth"; further on he states that, since the animal was one of a pair in the Trivandrum zoo, it is "therefore fully adult". There is equally some confusion over the sexes of the holotype and of its cage-mate in Trivandrum zoo. In the type description of *fergusoni* the female of the pair is stated to have been still alive in 1905, i.e., it is the male which is the holotype skin and skull.

But the label on the type specimen, skin and skull no. 0.5.26.16 identifies it as female; so does the entry in Lydekker's (1913) "Catalogue of ungulate mammals in the British Museum". The cage-mate's skull, no. 8.12.23.1, unsexed, has a label with the statement, "it has not yet been decided whether this specimen is the *type* skull or not" (of *fergusoni*); but seeing that Lydekker records 0.5.26.16 as the type in his own catalogue, this latter solution is probably correct.

The holotype, then, B.M. 0.5.26.16, is a juvenile female, with the second molars in process of eruption. The skin is a dark drab brown, with thick fleecy fur, inconspicuous white spots under the jaw, and the lower part of the forelimbs yellow-white with a black line down the front and rimming the hoofs; on the hindlimbs the same effect is seen, but less conspicuous and extensive. The paratype, 8.12.23.1, is a subadult with the third molars erupted but unworn, and the cranial sutures still widely open. The type skin can be placed squarely in the range of variation of the large type of Anoa, and the skulls accord well, age for age, with this assignment. Accordingly *Bos depressicornis fergusoni* falls as a synonym of *Bubalus (Anoa) depressicornis*.

In 1910, Ouwens received two living specimens of Anoa, and described them as a new species, *Anoa quarlesi*. The animals were from the mountains of the central Toradja region, Celebes, and were small in size, with woolly light brown coats and just small white spots above the hoofs; no white legs as in the large Anoa. Clearly, we have here the first description of the small species of Anoa, and so the small Anoa has to be known as *Bubalus (Anoa) quarlesi*.

The type description was published in French; the following year, in a different journal, a Dutch translation of it was published, together with an additional note on two further specimens of the new species. No reference was made to the 1911 description being just a translation of the 1910 one, and it is the later reference that is usually, though incorrectly, cited as the earliest use of the name *quarlesi*.

No further names have been applied to Anoa; Hooijer (1950) states that van Bemmelen considered *A. quarlesi* to have valid geographic races, but no new name or description has been forthcoming.

The full taxonomy and description of the subgenus *Anoa* is as follows:

### 1. *Bubalus (Anoa) depressicornis* (H. Smith, 1827). Lowland Anoa.

1827 *Antelope (Anoa) depressicornis* H. Smith, in Griffith, Cuvier's Animal Kingdom, 4 : 293. Celebes.

1853 *Oreas platyceros* Temminck, Esquisses zoologiques sur la côte de Guinée: 192.

1865 *Probubalus celebensis* Rütimeyer, Verhandl. naturf. Ges. Basel, 4 : 334.

1905 *Bos depressicornis fergusoni* Lydekker, Field, 106 : 378. No locality.

LOCALITIES : (1) Northern peninsula : Minahassa, Menado, Bambulan, Gorontalo (this study); Likupang, Lempias, coast near Limbe, forest between Langówan and Pángku, Paybi, Tolitoli (Heller, 1889). (2) Central Celebes: Donggala (this study). (3) Southeastern peninsula : north slope of Boro Boro

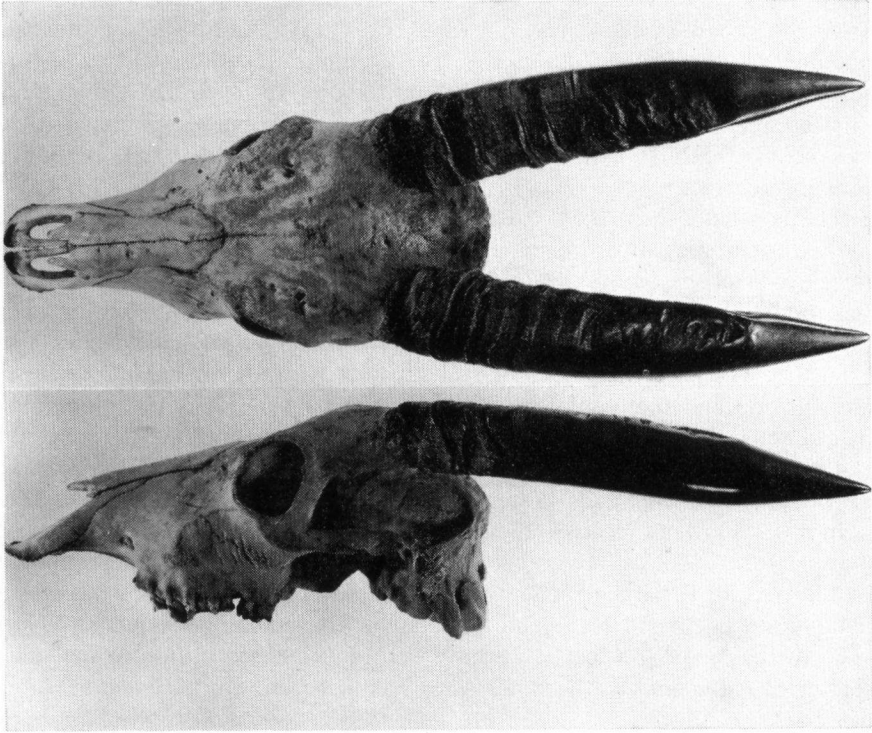


FIG. 3. *Bubalus (Anoa) depressicornis* H. Smith, 1827: old male skull, no locality: personal property of Mr Watze de Vries of Badhoevedorp. Skull length 304 mm; horn length 274 mm. The flattening and wrinkling process seen in the young adult male (see fig. 2) has been carried to extremes, and has advanced towards the tip of the horns — the usual effect of aging in this species.

Mts., Kampung Mowita (this study); Malili, Kolaka (Ouwens, 1910). (4) southwestern peninsula: caves north of Tjani "very recent", Panganrejang Tudeja "before 1300 A.D." (Hooijer, 1950).

DESCRIPTION: Colour of adult black, the hair being sparse, and the woolly brown juvenile coat lost about the time  $M_3^3$  is erupting. Legs are always white or yellowish-white, except for a black line down the front and across the pasterns. Groin light to white; often a white crescent on throat. Tail length 19.8—25.8% of total length (9 skins). Adult horn triangular in section flattened, with marked transverse ridges and a marked external keel; index of least to greatest (i.e. antero-posterior to bilateral) basal horn breadth, 57.9—80.0 in adult, 66.0—91.7 in juvenile, the marked expansion of the external angle occurring about the time of eruption of  $M_3^3$ . Skull length of male 298—322 mm, female 290—300 mm. Horn length of male 271—373 mm, female 183—260 mm. Toothrow length of both sexes 82—98. (See figs. 2 and 3).

B.M. 96.6.24.1 (Likupang), recorded by Lydekker (1913) as having "no white markings on the face or limbs" has an indistinct yellowish line down the inner sides of the limbs and on the outsides of the "knees", and a light coloured groin. Heller's specimen, Dresden 1816, has "einer greiser Anflug in der Umgebung aller Afterklauen und an der Innenseite der vorderen Phalangenglieder". These two specimens show the weakest expression of the white limb markings among sixteen skins of the species examined in the present study or described by Heller (1889).

## 2. *Bubalus (Anoa) quarlesi* (Ouwens, 1910). Mountain Anoa.

1910 *Anoa quarlesi* Ouwens, Bull. Dépt. Agric. Indes Néerl., 38 (Zool. 6): 7. Mountains of central Toradja district, Celebes.

1964 *Anoa anoa* Walker, Mammals of the World, 2: 1425. "Forested mountains of western Celebes". *Nomen nudum*.

LOCALITIES: (1) Northern peninsula: Besoa, Menado (this study). (2) Central Celebes: Lake Lindu, Tuwulu (this study). (3) Southeastern peninsula: Buton island (this study). (4) Southwestern peninsula: Latimodjong, Watampone, Madjene, mountains inland from Macassar at 2,000 m (this study); Toradja, Upper Binuwang, Palopa (Ouwens, 1910); Mandar Mts. (Mohr, 1921); Bola Batu "before 17th century", caves north of Tjani "very recent" — probably (Hooijer, 1950).

DESCRIPTION: Colour of adult dark brown to black, the hair sometimes still thick and woolly well into adulthood, especially in females, and even when the woolly coat is shed, hair is never as sparse as in *B. (A.) depressicornis*. Legs have only whitish or yellowish spots above the hoofs, and even these are often very inconspicuous or absent. Groin light but not white; never any white crescent on throat. Tail length 14.6—17.8% of total length (5 skins). Adult horns short and conical, rounded in section, just as in juveniles, with no marked ridges or external keel; index of least to greatest breadth, in both adult and juvenile, 84.4—106.3. Skull length of both sexes 244—290 mm. Horn length of both sexes 146—199 mm. Toothrow length of both sexes 65—80 mm. (See fig. 4).

ZMA (Amsterdam) no. 9294 is an infant male from Buton Island, off the southeastern peninsula. Although Ouwens (1911) refers to this specimen as belonging to *depressicornis*, the almost complete lack of pattern on the limbs makes it more probably that it is *quarlesi*, notwithstanding that in *depressicornis* at this age the pattern would be less developed than in an adult. This identification is important, as it extends the range of *quarlesi* which is not otherwise recorded from the southeastern peninsula.

ZMA 9292, an adult from Macassar, is striking in lacking any white markings anywhere. The weight is given on the label as 56 kg — apparently the only recorded weight for an Anoa.

RMNH (Leiden) no. 1178, from "Mountains behind Macassar", commented on by Hooijer (1950) because of its large size, is indeed a member of this species, although indeed the largest specimen recorded.

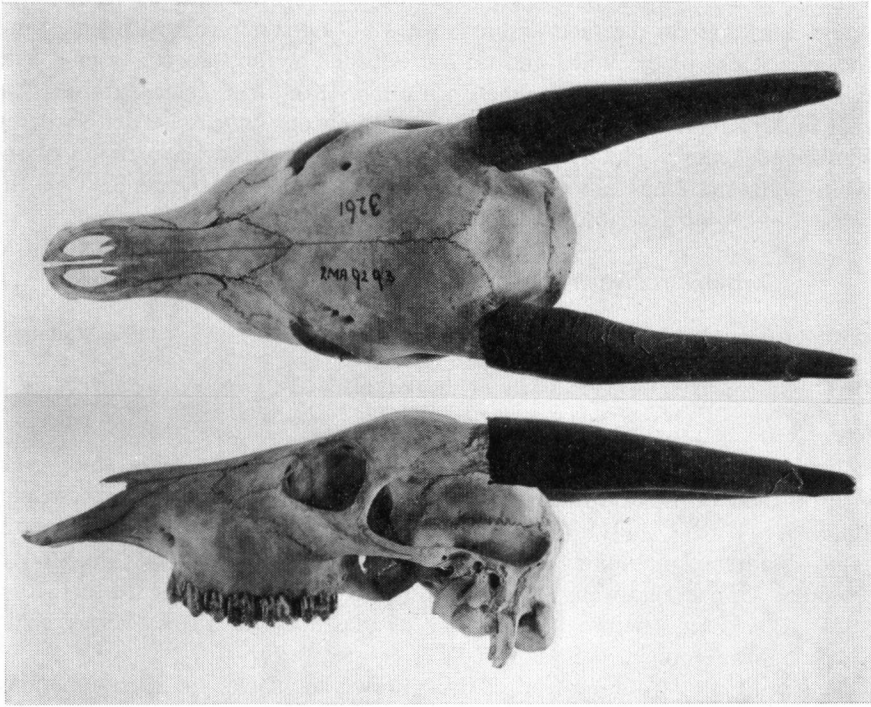


FIG. 4. *Bubalus (Anoa) quarlesi* Ouwens, 1910: young adult male skull from Menado, ZMA 9293. Skull length 246 mm; horn length 157 mm. Notice the conical horns, rounded in section, with no lateral expansion of the external edge (which is weakly marked).

The type specimens of Ouwen's species were not adult; hence his description gives an exaggerated idea of the size difference between *B. (A.) quarlesi* and *B. (A.) depressicornis*. Three specimens in the Amsterdam Museum, formerly in the Ouwens collection at Buitenzorg, are labelled as syntypes; one (ZMA 9295) is an infant and skull, and is probably not a type; judging from the relative sizes of Ouwen's types, it is most likely that ZMA 9288 (Juvenile I, skin and skull) is the male and ZMA 9289 (Juvenile II, skin and skull) the female. Since Ouwens mentions only two specimens in his paper, the labelling of three as syntypes is a little puzzling.

The localities given by Mohr (1921) for the two species quoted from P. & F. Sarasin (1905), cannot be taken as certain, since the Sarasins were merely trying to assess the distribution of Anoa in general and did not distinguish different types. Mohr's allocation of the locality records to one species or the other seems to have been based on likelihood as assessed from previous definite records.

Some recent works, noticeably Walker (1964), refer to the Tamarao of Mindoro Island (Philippines) as a member of the genus *Anoa*. In the present



Table I. Specific differences at corresponding ages: subgenus *Anoa*. (Infant — no permanent teeth present; juvenile I —  $M_1^1$  present; juvenile II —  $M_2^2$  present; young adult — all permanent dentition, but  $M_3^3$  unworn).

	<i>Bubalus (Anoa)</i> <i>depressicornis</i>	<i>Bubalus (Anoa)</i> <i>quarlesi</i>
SKULL LENGTH		
Infant	—	203.5 mm (2)
Juvenile I	229.0 (1)	201.0 (1)
Juvenile II	263.5 (2)	242.3 (3)
Young Adult	293.0 (1)	259.3 (10)
Adult female	295.0 (4)	
Adult male	306.8 (7)	
HORN LENGTH		
Infant	—	42.5 (2)
Juvenile I	87.0 (1)	77.0 (1)
Juvenile II	151.0 (2)	141.7 (3)
Young adult	188.5 (2)	161.0 (16)
Adult female	216.9 (18)	
Adult male	296.4 (15)	
HORN INDEX		
Infant	—	98.4 (2)
Juvenile I	104.3 (1)	100.0 (1)
Juvenile II	89.4 (2)	86.2 (3)
Young adult	90.3 (2)	96.9 (12)
Adult female	70.5 (4)	
Adult male	67.1 (7)	
BODY LENGTH		
Juvenile I	—	1070 (1)
Juvenile II	—	1220 (2)
Young adult	1610 (1)	1524 (2)
Adult female	1887 (1)	
Adult male	1700 (1)	
HEIGHT (WITHERS)		
Juvenile I	700 (1)	625 (1)
Juvenile II	—	623 (2)
Young adult	757 (2)	690 (1)
Adult	860 (1)	
COLOUR		
Infant	Golden brown (1)	Golden brown (2)
Juvenile I	Drab-brown (1)	Golden to red-brown (2)
Juvenile II	Medium brown (1)	Light to dark brown (4)
Young adult	Brown to black (2)	Dark brown to black (7)
Adult	Black (7)	

Table II. Geographic variation in subgenus *Anoa*. (Means and Standard Deviations).

	Skull length	Horn length	Biorbital breadth
<i>B. (A.) depressicornis</i> (♂)			
Minahassa	309.0 ± 8.4 (6)	296.0 ± 13.0 (17)	128.6 ± 6.5 (6)
Donggala	296 (1)	195 (1)	119 (1)
<i>B. (A.) quarlesi</i>			
Besoa, Menado	251.0 ± 7.3 (4)	146.0 ± 8.9 (4)	103.4 ± 3.0 (4)
Lindu, Tuwulu		161.4 ± 10.5 (5)	
Macassar, Madjene	264.8 ± 14.3 (6)	176.0 ± 9.0 (6)	110.7 ± 3.5 (6)

Table III. Limb proportions: genus *Bubalus*.

(1) Compared to metacarpal length (following Heller, 1889).

	<i>B. (B.) arnee</i> (1)	<i>B. (B.) mindorensis</i> (1)	<i>B. (A.) depressicornis</i> (3)	<i>B. (A.) quarlesi</i> (2)
Humerus	1.8	1.9	1.8	1.5—1.7
Radius	1.6	1.8	1.5—1.6	1.6
Femur	2.1	2.3	1.9—2.1	1.9—2.0
Tibia	1.9	2.1	1.9—2.0	2.0—2.1
Metatarsal	1.1	1.2	1.1	1.1

(2) Metapodial breadth to length

Metacarpal	38.0	45.8	29.1—35.4	30.8—31.0
Metatarsal	31.6	32.0	—	24.6—24.4

(3) Humerus length 442 253.5 210 —230 174 —184

system, however, in which *Anoa* is made a subgenus of *Bubalus*, the Tamarao is not regarded as belonging to this subgenus. Indeed Bohlken (1958) made the Tamarao a subspecies of the large Asiatic Buffalo, calling it *Bubalus arnee mindorensis*; in the present author's opinion, however, the Tamarao should be allowed specific rank on morphological grounds: it is much smaller and more robust than *Bubalus arnee*, with not only short thick horns, but shortened and thickened distal segments to the limbs. But that it is a member of subgenus *Bubalus*, not of subgenus *Anoa*, there can be no doubt: the general shape of the horns, with a considerable outward initial direction, completely different from the closely approximated and backwardly directed horns of the Anoa; the stocky limbs; the reduced parietal; the narrow occipital; and the tooth characters — all these features confirm the position of *Bubalus mindorensis* in the subgenus *Bubalus*.

The possibility of subspeciation in the two species of Anoa cannot be confirmed as yet, due to lack of specimens; as table II shows, however, there seem to be some geographically determined size differences within the two species, which with more specimens might prove significant. No external differences are apparent.

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