2016

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Disciplines

Medicine and Health Sciences | Social and Behavioral Sciences

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Abstract

Celebochoerus is a unique suid having extremely large upper tusks, and which was to date only known from the Pliocene-Pleistocene of Sulawesi Island in Indonesia. Here, we report on the discovery of a canine fragment referable to *Celebochoerus* from the Cagayan Valley of Luzon, Northern Philippines. We name a new species, *Celebochoerus cagayanensis* nov. sp., which differs from the Sulawesi species *Celebochoerus heekereni* in having mesial and distal enamel bands on the upper canines. We see these characteristics as symplesiomorphic in suids and propose a migration route from the Philippines to Sulawesi, possibly out of Taiwan, which would have occurred independently from the better known Pleistocene migration route from India into Java.

1. Introduction

The Cagayan Valley (Northern Luzon Island, Philippines; Fig. 1) is known for its Pleistocene fauna (von Koenigswald, 1956) since 1936 (Beyer, 1947: p. 214). The fossil fauna has been associated, somewhat questionably, with the ''Cabalwanian'' pebble tools (von Koenigswald, 1958). The long history of archaeological surveys and excavations in this area (Tobias, 1999) has yielded a considerable collection of fossils, including very few Suidae remains, which have remained largely undescribed (von Koenigswald, 1956; de Vos and Bautista, 2003; Liscaljet, 2012). We report here on the surface discovery of a suid upper canine fragment during one of our recent (2012) surveys in the Cagayan Valley. Based on its morphology we attribute this specimen to a new species: *Celebochoerus cagaya- nensis* nov. sp., and review the paleobiogeography of the genus.

In his description of the Pleistocene fauna from the Philippines, von Koenigswald (1956: p. 314) reported, with regard to suids, that only a modern boar tusk from an Iron Age layer in Novaliches was known. A few years later in his description of the Cabalwanian industry, von Koenigswald (1958) mentioned the existence in the National Museum collections of *Sus* along with elephant and tektites from Anda (Pangasinan province), but without further details. Since Beyer (1955) does not mention *Sus* specimens among the Pleistocene mammal finds in the Philippines, the suid specimen referred to by von Koenigswald (1958) was almost certainly found in 1957. The only other mention of Suidae from Pleistocene layers of the Philippines was made by Fox and Peralta (1974: p. 100) under a generic reference of "pigs" found on the surface during a survey on the western side of the Cagayan Valley, along the Pleistocene anticlines. As part of the same Early Man Project in Cagayan Valley, Mathisen (1981: p. 125) reported

the discovery of pig on the northeastern flank of the Panggul anticline (Fig. 1). Fox and Peralta (1974) commented that those collections would be studied by D.A. Hooijer. However, to the best of our knowledge, Hooijer never published about them and appears not to have ever studied these collections.

While studying the entire Pleistocene faunal collection present in the National Museum of the Philippines, de Vos and Bautista (2003) were the first to describe all of the Suidae teeth, which only included three isolated lower left third molars. They noted that the Suidae specimens were labelled: "new species *C. cagayanensis*". They nevertheless concluded that "although they look similar to *Celebochoerus*, as there are only three lower molars, it is, based on three specimens, not wise to give a specific determination. So, the best option is to indicate the molars as *Sus* sp." (de Vos and Bautista, 2003: p. 17). Excavations subsequently conducted in the Cagayan Valley (Bondoc, 1979) did not yield any additional suid remains (Bautista and de Vos, 2001; Jago-on, 2009). Apart from our own survey resulting in the newly-discovered upper canine fragment, the three lower left third molars labelled as "*C. cagayanensis*" remained the only other known suid fossils, which have never been described before.

The genus *Celebochoerus* was erected by Hooijer (1948) based on some characteristic upper canine specimens collected by H.R. van Heekeren in the Walanae Valley in Southwest Sulawesi, Indonesia (Fig. 1). The diagnosis for the genus and species *Celebochoerus heekereni* was based on a left upper canine (Hooijer, 1948). In the following years, more complete descriptions of this taxon were given, based on additional finds of teeth and postcranial remains (Hooijer, 1951, 1954). According to Hooijer (1950) the *Celebochoerus* incisors are similar to those of *Sus*, but in van der Made's assessment (1997) these incisors differ from *Sus* in being wider, while the premolars are more akin to those of *Potamochoerus*. Our assessment of the *Celebochoerus* molars, however, indicates they are very simple, more similar to those of *Babyrousa*, and quite distinct from *Sus*.

The most distinctive characteristics of *Celebochoerus* are the very large upper canines that are much wider than those of the extant endemic suids of Sulawesi, *Sus celebensis* and *Babyrousa celebensis*, with the permanent canines of the latter being devoid of any enamel. Hooijer (1950) noted some sexual dimorphism in *C. heekereni* with the females having canines three-fourths as large as those of males, a feature that was later contested by Aziz (1990: p. 40). Later it was noted that size-based sexual dimorphism can only be distinguished when comparing individuals from the same locality, since the average size of the dentition appears to decrease with time (van den Bergh and Aziz, 1995). Taken together, these characteristics, as well as some distinctive cranial features (Suyono, 2009), make *C. heekereni* unique among Suidae, and apart from our excavation, had only been found in Sulawesi.

Pickford (1993) considers *Celebochoerus* as a sister taxon to *Sus* and *Babyrousa* and positions it as a possible ancestor to the latter, with all three genera being grouped as a basal lineage of the Suini tribe. Classification of *Celebochoerus* among Suinae is not, however, consensual. Van der Made (2010) views *Celebochoerus* as a babyrousine together with *Babyrousa* and *Potamochoerus*. We follow here the classification of Pickford (1993) that is also followed by Harris and Li-Ping (2007). The origin of *Celebochoerus* remains unclear. A cladistic analysis including *Celebochoerus* remains to be undertaken. Some authors proposed *Propotamochoerus* from the Pliocene Tatrot layers of the Indian Siwaliks as the most probable ancestor (Hooijer, 1954; Thenius, 1970; Suyono, 2009), while Aziz (1990) sees some relations with *Phacochoerus* given the large tusks and several other cranial characteristics, but we think the superficial resemblance with the latter should be attributed to evolutionary convergence.

The proposed phylogenetic trees of *Celebochoerus* appear to be strongly influenced by an assumed geographical origin. Hooijer (1950: p. 7) considered the Sulawesi Pleistocene fauna as a whole and reprinted De Terra et al.'s (1941: p. 460) map, a map also used by Movius (1948) to show two possible migration routes, one from India via the exposed Sunda Shelf to Java, and a second one from China to Sulawesi via Taiwan and the Philippines. Von Koenigswald (1956) favored a Chinese origin for the Sulawesi fauna based on his study of the Pleistocene fauna from the Philippines. Braches and Shutler (1984) and Heaney (1985) refuted the existence of the China migratory route, favoring instead an Indian-Javanese connection, with Borneo-Palawan as the main gate to Sulawesi. The debate remains unresolved, making the reporting of even fragmentary new Pleistocene fossil discoveries, such as the one we present here, a noteworthy contribution.

2. Systematic paleontology

For the description of the teeth we follow the nomenclature of van der Made (1996).

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Suborder Suina Gray, 1868
Family Suidae Gray, 1821
Subfamily Suinae Gray, 1821
Tribe Suini Gray, 1821
Genus *Celebochoerus* Hooijer, 1948
Celebochoerus cagayanensis nov. sp. Ingicco
Figs. 2 and 3
1958. *Sus* – von Koenigswald, p. 69.
1974. Pigs – Fox and Peralta, p. 100.
2003. *Sus* sp. – de Vos and Bautista, p. 17.

Derivation of the name: refers to the Cagayan Valley (Luzon Island, Philippines) where the holotype (a canine specimen) comes from.

Holotype: II-2014-J1-006, the base of a fragmentary upper left canine broken at both ends (Fig. 2). The fragment is in two pieces that have been refitted (30% solution of paraloid B-66).

Type locality and horizon: Southern extremity of the Cabalwan anticline (17833'45.03"N, 121833'35.74" E), Rizal Municipality, Kalinga Province, Northern Luzon Island, the Philippines, within the Awidon Mesa Formation, Middle Pleistocene relative age.

Repository: The Archaeology Division of the National Museum of the Philippines in Manila.

Material: NMP 182a and b (Fig. 3(A, B)): two lower left third molars from Espinosa Ranch, Liwan, Kalinga-Apayao, 1971; collector: S.M. Lopez. NMP 398a (Fig. 3(C)): lower right M3, Locality Cab III-23, Solana, Cagayan, March-May 1978; collector: ISU-National Museum. All specimens are stored in the Geology Division of the National Museum of the Philippines in Manila.

Measurements (holotype): 50.5 x 29.5 x 21.5 mm.

Diagnosis: Large upper canine with oval cross-section. Compressed vestibulolingually. Presence of enamel bands forming two to three thin ridges on the mesial and distal sides of the canine. Deep and wide mesial longitudinal groove.

Differential diagnosis: Differs from *Celebochoerus heekereni* in the presence of enamel bands on the mesial and distal surfaces of the upper canine. *C. heekereni* upper canines are sub-triangular in cross-section (Hooijer, 1948), although Aziz (1990) recognizes three types of cross-sections in this species, one of which is kidney- shaped. *Sus*, *Potamochoerus* and *Babyrousa* all have a sub-oval cross-section of the upper canines. The mesial longitudinal groove is shallow in *C. heekereni*. *C. heekereni* has larger upper canines although reduction in size through time seems to occur in this species (van den Bergh, 1999). The third lower molars are the same as in *C. heekereni* but are missing the pentapostcristid.

3. Discussion

Based on detailed geological mapping, recording of stratigraphic sections, paleomagnetic dating, marine microfossil stratigraphy, and faunal assemblages from single localities, van den Bergh and Aziz (1995), van den Bergh (1999), and de Vos et al. (2007) propose three subsequent migrations into Southwest Sulawesi (which is considered to have been a separate island until mid-Pleistocene times). The first migration occurred before the onset of the Pleistocene and included *Celebochoerus* and two pigmy proboscideans. During the Middle Pleistocene a medium-sized *Stegodon* and a large-bodied and high-crowned *Elephas* species were present in South Sulawesi, replacing the two pygmy proboscideans. Modern fauna elements such as *Bubalus* (*Anoa*), *Babyrousa* and *Sus celebensis* are not present until the Late Pleistocene, when *Celebochoerus* appears to have become extinct, with the youngest proven occurrence dating to a minimum age of 200 ka (van den Bergh et al., 2016). While all authors seem to agree that the current evidence does not support the former existence of any land bridges between the Philippines and Sulawesi, an overseas migration route during the Pleistocene has been favored by several (De Terra et al., 1941;

Hooijer, 1951; von Koenigswald, 1956; Sartono, 1973; Aziz, 1990; van den Bergh, 1994), but questioned by others (Groves, 1976, 2001; Braches and Shutler, 1984; Heaney, 1985).

The discovery of a new species of *Celebochoerus* in northern Luzon is undoubtedly an important clue for a Filipino origin of at least part of the Sulawesi fauna, given this genus is absent from the well-documented Javanese fossil record. Fossils other than *Celebochoerus heekereni* also attest for this migration route, such as the *Stegodon* fossils found in Sangihe Island (Aziz, 1990), which is located midway between the north of Sulawesi and the south of the Philippines. The Sangihe *Stegodon* is also very similar to the *Stegodon* sp. B originating from the Tanrung Formation in South Sulawesi (van den Bergh, 1994).

The geology of the Cagayan Valley has been studied in detail by Mathisen (1981). The Awidon Mesa Formation from where the *Celebochoerus* fossils originate is composed of dacitic tuffaceous fluvial sediments (sandstones and claystones) and mudflows, with frequent beta-quartz, euhedral hornblende and sodic feldspar, deposited within a distal alluvial fan (Fig. 1). Tektites and vertebrate fossils are very common in this fluvial volcaniclastic formation (Lopez, 1972). The Pleistocene Awidon Mesa formation unconformably overlies the Pliocene Ilagan Formation that is composed of interbedded sandstones and mudstones, and underlies more or less recent river terraces (Lopez, 1972; Mathisen, 1981). No absolute date has ever been successfully obtained for the Cagayan Valley Formations, but a Middle Pleistocene age has been proposed for the Awidon Mesa beds based on the recovery of extinct megafauna (Mathisen, 1981: p. 40).

Our proposed biochronological correlation between the Cagayan Valley and the Walanae Valley is tentative. In Sulawesi, most of the *C. heekereni* fossils originate from the Early Pleistocene Beru Member and a few (Suyono, 2009) from the Tanrung Formation of estimated Middle-Late Pleistocene age (van den Bergh, 1999; Fig. 1). Three samples (one molar of *Elephas celebensis* and two molars of *C. heekereni*) from the Beru Member were ESR- dated to widely spread ages of 2.1 Ma to 0.5 Ma (van den Bergh, 1999). Because the external dose was not calculated, those dates have to be regarded with extreme caution. The paleomagnetic results are nevertheless consistent with an old age for the Beru Member (van den Bergh, 1999: p. 128). The Beru Member of the Walanae Formation is composed of fluvio-estuarine sandstones (lower subunit A) and fluvial deposits (upper subunit B) (van den Bergh and Aziz, 1995). van den Bergh (1999: p. 124) mentions that the few *Celebochoerus* remains from the Tanrung Formation (a terrestrial conglomerate locally overlying the Walanae Fm. unconformably east of the Wallanae Valley; Fig. 1) have a rolled aspect and may be reworked from older strata. More recently, uranium-series dating on eight *Celebochoerus* teeth and bones from the archaeological site Talepu, which pertains to the upper subunit B of the Beru Member, were obtained. The combined results returned a minimum age of 200 ka (van den Bergh et al., 2016), though van den Bergh (1999) nevertheless recognizes two species of *Celebochoerus*: the typical *C. heekereni* ranging throughout the Beru Member up to the Tanrung Formation, and an unnamed short-legged species which has so far only been recorded from the upper part of subunit B of the Beru Member. Based on this information, the Cagayan *Celebochoerus* species is most likely younger in age than the oldest record of the Sulawesi species but older than the youngest occurrence of the latter.

The *Celebochoerus* fossils from the Tanrung fauna, which is probably younger than the lower part of the Beru Member of the Walanae Formation, are on average slightly smaller than the ones from the Beru Member (van den Bergh et al., 2001). This observation also applies to the canines (van den Bergh, 1999). Fig. 4 shows measurements of *C. cagayanensis* nov. sp. as compared to several specimens published by Hooijer (1954) from the van Heekeren collections and several unpublished *Celebochoerus* upper canines from Sulawesi excavated over a number of years by one of us (GvdB). Details on those measurements are listed in Table 1. The oldest specimens, found associated with the pygmy *Stegoloxodon celebensis* (formerly named *Archidiskodon celebensis*) at the locality Sompe and with both *Sl. celebensis* and *Stegodon sompoensis* at the locality Lonrong, are the largest. The more recent specimens from Lakibong 1 and Lakibong 2, also associated with *Sl. celebensis* and *St. sompoensis*, are smaller. As stated previously, the youngest specimens from Tanrung that were found associated with the dwarf *Stegodon* sp. B (larger-bodied than *St. sompoensis*) and a large high-crowned *Elephas*, are among the smallest specimens measured so far (Fig. 4). Based on its size, *C. cagayanensis* nov. sp. groups with the smallest and most recent specimens of *Celebochoerus* from Sulawesi. *C. cagayanensis* nov. sp., however, is distinct from the Sulawesi specimens by its more compressed vestibulo-lingual diameter, although some variations occur within *C. heekereni* (Fig. 4) – which is not surprising considering the long time-range spanned by *Celebochoerus*. The outer radius of curvature of *C. cagayanensis* nov. sp. canine is 37 mm and the inner radius of curvature is 30 mm, resulting in a curvature index (inner radius/transverse diameter x100) of 139.5. These measurements cluster *C. cagayanensis* nov. sp. among the

small Suidae species (van der Made, 1996).

We also consider here that the three molars from the National Museum collections (Fig. 3) can now be securely attributed to *C. cagayanensis* nov. sp., and thus compare them to the Sulawesi specimens. Fig. 5 reproduces de Vos and Bautista's (2003) observations of the slender size of the Cagayan species compared to the Sulawesi specimens. Clustering with the smaller variety of *Celebochoerus heekereni* from Lakibong-2, *Sus oliveri* and *Sus philippensis*, the Philippine *C. cagayanensis* nov. sp. also appears to be among the smallest of the island endemic suids, when taking into consideration both fossils from Java and Sulawesi and extant specimens from the Philippines.

The three third lower molars from Cagayan Valley (Fig. 3) are all similar to *C. heekereni* in their simpler morphology as compared to *Sus scrofa*, as previously noted by Hooijer (1954). Apart of their slightly slenderer aspect compared to *C. heekereni* (Table 2), the Cagayan molars also display very thick and weakly wrinkled enamel, and round cusps. The third lower molar is composed of five main cusps and six additional small crests. This morphotype is the simplest form described by van der Made (1996: p. 7). Behind the first pair of cuspids are a well-developed metaendoconulid and an even larger hypoprecristid such as in *C. heekereni*. A small hypoectoconulid is also present on the buccal side of the trigonid. Behind the second pair of cuspids are a pentaprecristid as large as the pentaconid; a small pentaectoconulid is present on its buccal side. On the lingual side of the pentaconid a pentaendoconulid is also present. The third lower molars of *C. cagayanensis* nov. sp. are therefore similar to the *C. heekereni* molars, with the exception of the presence of a pentapostcristid, which is not developed in the Philippine species.

C. cagayanensis nov. sp. further very distinctively differs from *C. heekereni* in having enamel bands on the mesial and distal aspects of the canine (Fig. 2). Enamel on the mesial and distal aspects of the upper canines is also present, but more developed, in *Sus* and *Potamochoerus*. This characteristic can therefore be viewed as symplesiomorphic in suines. Although most likely younger than (or at least coeval with) the Sulawesi specimens, *C. cagayanensis* nov. sp. seems to be more archaic in this aspect. With such a fragmentary specimen, any phylogenetic assessment remains tentative, but the ancestors should probably be sought either in Taiwan or Java. The molars of *Celebochoerus* from the Philippines or from Sulawesi are much simpler than the ones of the contemporaneous Javanese fossil species *Sus macrognathus* and *Sus brachygnathus* (Hardjasasmita, 1987). Based on four isolated second molars, Guq-Qin et al. (1999) described *Potamochoerus* aff. *hyotherioides* Pearson, 1928 from the Early-Middle Pleistocene Chochen Formation of Taiwan. The taxonomic status of these fossils is beyond the scope of this article, but we notice that the Taiwanese *Potamochoerus* is described as having simple molars like the two *Celebochoerus* species (Hooijer, 1954; de Vos and Bautista, 2003). These Taiwanese fossils could well be related to *Celebochoerus*, but at this time the fragmentary preservation of *C. cagayanensis* nov. sp. precludes any cladistic analysis to test this hypothesis.

Although current evidence indicates that the two *Celebochoerus* species appear closer to the contemporaneous Taiwanese Suidae than to the Sundaic species for their comparable simpler molar patterns, at this time we cannot reject an Indonesian migration route into the Philippines. Beyond a Northern colonization via Taiwan, that has been favored by some Murinae and *Crocidura* species (Jones and Kennedy, 2008; Esselstyn et al., 2010), three migration routes have been highlighted by recent phylogenetic studies: two Western routes from Borneo, including a Northwest- ern route via Palawan and a Southwestern one via Sulu, and a third Southern route from Sulawesi via the Sangihe Islands (Brown et al., 2013). The possible passage between Taiwan and the Philippines has long been dismissed for its longer distance and deeper waters than the water barrier between Borneo and Palawan, which was the situation even during the major marine regression periods. This distance is nevertheless not longer than that between the Philippines and Sulawesi. Furthermore, as shown by Sondaar (1977) and Johnson (1980), and more recently by Aziz et al. (1995) regarding the origin of the fauna of Sulawesi, there is no need for any land bridge for island colonization by proboscideans because these animals can swim very well over long distances. The same is also true for suids (van der Made et al., 2006), and a broken land bridge would suffice to allow for a sweepstake migration route.

4. Conclusion

The discovery of a new species of *Celebochoerus* herein named *C. cagayanensis* nov. sp. in northern Luzon adds to our knowledge of this genus, which previously was only known from one formally described species – *C. heekereni*. It also provides a clue for a Philippine origin of at least part of the Sulawesi fauna given that this genus is absent from the well-documented fossil record of Java. Because there is no strong evidence for any faunal

similarity between Sulawesi and Java so far, we prefer the out-of-Taiwan via the Philippines hypothesis for the Sulawesi fauna, although we cannot firmly reject a Sundaic origin. This could have happened sometime around the Pliocene-Pleistocene transition, as *Celebochoerus* is present in the oldest fossiliferous layers of the Walanae Valley. In addition, the migration between the Philippines and Sulawesi could have occurred in both directions, and the rough geological age for *C. cagayanensis* nov. sp. and the Sulawesian specimens should not be considered as an argument in favor of a South-North migration. Furthermore, some characteristics de- scribed here, such as the mesial and distal enamel bands on the canine and the absence of a pentapostcristid, makes *C. cagayanensis* nov. sp. more archaic than *C. heekereni*.

References

Aziz, F., 1990. Pleistocene mammal faunas of Sulawesi and their bearing to paleo- zoogeography (Ph.D. Thesis). Kyoto University, Japan.

Aziz, F., van den Bergh, G., Sondaar, P.Y., de Vos, J., 1995. Vertebrate paleontology. In: The Geology and Stratigraphy of the Vertebrate-Bearing Deposits in the Sengkang Basin: the Terrestrial Faunal Evolution of South Sulawesi during the Late Pliocene and Quaternary. Geological Research and Development Centre, Bandung 50–53. Bautista, A.P., de Vos, J., 2001. Archaeological exploration and excavation at Solana, Cagayan (No. Progress Report NO. 4) National Museum of the Philippines, Manila.

van den Bergh, G.D., 1999. The Late Neogene elephantoid-bearing faunas of Indonesia and their palaeozoogeographic implications. Scr. Geol. 117, 430.

van den Bergh, G.D., de Vos, J., Sondaar, P.Y., 2001. The Late Quaternary palaeogeo- graphy of mammal evolution in the Indonesian Archipelago. Palaeogeography Palaeoclimatology Palaeoecology. Scripta Geologica 171, 385–408.

van den Bergh, G.D., 1994. The first *Stegodon* fossils from Central Sulawesi and a new advanced *Elephas* species from South Sulawesi. Geologcial Research and Development Centre Bulletin 17, 22–39.

van den Bergh, G.D., Aziz, F., 1995. Geologcial Setting. In: The Geology and Stratigraphy of the Vertebrate-Bearing Deposits in the Sengkang Basin: the Terrestrial Faunal Evolution of South Sulawesi during the Late Pliocene and Quaternary. Geological Research and Development Centre, Bandung 8–13.

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., Suyono, Storey, M., Setiabudi, E., Morwood, M.J., 2016. Earliest hominin occupation of Sulawesi, Indonesia. Nature 529, 208–211.

Beyer, H.O., 1955. New finds of fossil mammals from the Pleistocene strata of the Philippines. National Research Council and Philippine Geological Society, Manila.

Beyer, H.O., 1947. Outline review of Philippine archaeology by islands and provinces. Philippine Journal of Science 77, 205–390.

Bondoc, N.H., 1979. A re-investigation of the Espinosa archaeological sites Cagayan and Kalinga-Apayao. Anthropological Papers of the National Museum of the Philippines 6, 1–26.

Braches, F., Shutler Jr., R., 1984. The Philippines and Pleistocene dispersal of mammals in Island Southeast Asia. Philippine Quarterly of Culture and Society 12, 106–115.

Brown, R.M., Siler, C.D., Oliveros, C.H., Esselstyn, J.A., Diesmos, A.C., Hosner, P.A., Linkem, C.W., Barley, A.J., Oaks, J.R., Sanguila, M.B., Welton, L.J., Blackburn, D.C., Moyle, R.G., Peterson, A.T., Alcala, A.C., 2013. Evolutionary processes of diversification in a model island archipelago. Annual Reviews in Ecology and Evolution and Systematics 44, 411–435.

De Terra, H., Movius Jr., H.L., Colbert, E.H., Bequaert, J., 1941. Research on early Man in Burma, with supplementary reports upon the Pleistocene vertebrates and mollusks of the region, and Pleistocene geology and early Man in Java. Transactions of the American Philosophical Society, new series 32, 263–464.

Esselstyn, J.A., Oliveros, C.H., Moyle, R.G., Peterson, A.T., McGuire, J.A., Brown, R.M., 2010. Integrating phylogenetic and taxonomic evidence illuminates complex biogeographic patterns along Huxley's modification of Wallace's Line. Journal of Biogeography 37, 2054–2066.

Fox, R.B., Peralta, J.T., 1974. Preliminary report on the Palaeolithic archaeology of Cagayan valley, Philippines, and the Cabalwanian industry. In: Proceedings of the 1st Regional Seminar on Southeast Asian Prehistory and Archaeology, June 26–July 4 1972, pp. 100–147.

Groves, C.P., 2001. Mammals of Sulawesi: where did they come from and when, and what happened to them when they got there? In: Metcalfe, I., Smith, J.M.B., Morwood, M., Davidson, I. (Eds.), Fauna and floral migrations and evolution in SE Asia-Australasia. AA Balkema, Lisse, pp. 334–342.

Groves, C.P., 1976. The origin of the mammalian fauna of Sulawesi (Celebes). Sonderdruck aus Z.f. Saügetierkunde 41, 201–216.

Guq-Qin, Q., Chuan-Kun, H., Chun-Hsiang, C., 1999. The Pleistocene fossil suids from Chochen, Tainan, Southwestern Taiwan. Bulletin of the National Museum of Natural Science 12, 33–40.

Hardjasasmita, H.S., 1987. Taxonomy and phylogeny of the Suidae (Mammalia) in Indonesia. Rijksmuseum van Geologie en Mineralogie 85, 1–68.

Harris, J.M., Li-Ping, L., 2007. Superfamily Suoidea. In: Prothero, D.A., Foss, S.E. (Eds.), The evolution of artiodactyls. JHU Press, Baltimore, pp. 130–150.

Heaney, L.R., 1985. Zoogeographical evidence for Middle and Late Pleistocene land bridges to the Philippines islands. Modern Quaternary Research in Southeast Asia 9, 127–143.

Hooijer, D.A., 1948. Pleistocene vertebrates from Celebes I. *Celebochoerus heekereni* nov. gen. nov. spec. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 51, 1024–1032.

Hooijer, D.A., 1949. Pleistocene vertebrates from Celebes VIII. Dentition and skeleton of *Celebochoerus Heekereni* Hooijer. Zoologische Verhandelingen 24, 1–52.

Hooijer, D.A., 1954. Pleistocene vertebrates from Celebes VIII. Dentition and skeleton of *Celebochoerus heekereni* Hooijer. Zoologische Mededelingen 24, 1–46.

Hooijer, D.A., 1951. Pygmy elephant and giant tortoise. The Scientific Monthly 72, 3–8.

Hooijer, D.A., 1950. A further note on the canine of *Celebochoerus*. Zoologische Mededelingen 21, 307–309.

Jago-on, S.C., 2009. Report on the archaeological excavation and exploration in Cagayan Valley (Early Man Project). Proceedings of the Society of Philippine Archaeologists 7, 37–60.

Johnson, D.L., 1980. Problems in the land vertebrate zoogeography of certain Islands and the swimming powers of elephants. Journal of Biogeography 7, 383–398.

Jones, A.W., Kennedy, R.S., 2008. Evolution in a tropical archipelago: comparative phylogeography of Philippine fauna and flora reveals complex patterns of colonization and diversification. Biological Journal of the Linnean Society 95, 620–639.

Liscaljet, N., 2012. Napakaliit trompa: new pygmy pproboscidea remains from the Cagayan valley (Philippines). Quaternary International 276–277, 278–286.

Lopez, S.M., 1972. Contributions to the Pleistocene geology of Cagayan valley, Philippines, I. Geology and Palaeontology of Liwan Plain. In: Seminar on South-east Asian Prehistory and Archaeology, June 26–July 3.

van der Made, J., 1996. Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. Contributions to Tertiary and Quaternary Geology 33, 3–254.

van der Made, J., 2010. The pigs and "Old World peccaries" (Suidae and Palaeochoeridae, Suoidea, Artiodactyla) from the Miocene of Sandelzhausen (southern Germany): phylogeny and an updated classification of the

Hyotheriinae and Palaeochoeridae. Paläontologische Zeitschrift 84, 43–121.

van der Made, J., Morales, J., Montoya, P., 2006. Late Miocene turnover in the Spanish mammal record in relation to palaeoclimate and the Messinian Salinity Crisis. Palaeogeography, Palaeoclimatology, Palaeoecology 238, 228–246.

Mathisen, M.E., 1981. Plio-Pleistocene geology of the Central Cagayan valley, Northern Luzon, Philippines. Iowa State University, Ames, Iowa.

Movius Jr., H.L., 1948. The Lower Palaeolithic cultures of Southern and Eastern Asia. Transactions of the American Philisophical Society, New Series 38, 327–420.

Pickford, M., 1993. Old World Suoid systematics, Phylogeny, biogeography and biostratigraphy. Paeleontologia y Evolucio 26–27, 237–269.

Sartono, S., 1973. On Pleistocene migration routes of vertebrate fauna in Southeast Asia. Geological Society of Malaysia Bulletin 6, 273–286.

Sondaar, P.Y., 1977. Insularity and its effect on mammal evolution. In: Farris, J.S. (Ed.), Major Patterns in Vertebrate Evolution. Plenum Press, New York, pp. 1–37.

Suyono, 2009. The study of fossil faunas in the Wallanae Basin, Indonesia. University of Wollongong, 169.

Thenius, E., 1970. Zur Evolution und Verbreitungsgeschichte der Suidae (Artiodactyla, Mammalia). Zeitschrift für Saugetierkunde 35, 321–384.

Tobias, C.M., 1999. Archaeological history of Cagayan Province. Hukay 2, 8–31. Von Koenigswald, G.H.R., 1956. Fossil Mammals from the Philippines. In: Natl. Res. Counc. Philipp. Pap. 22 Proc. Fourth Far-East. Prehistory Congress. pp. 1–14.

Von Koenigswald, G.H.R., 1958. Preliminary report on a newly-discovered Stone Age culture from Northern Luzon, Philippine Islands. Asian Perspectives 2, 69–71.

de Vos, J., Bautista, A., 2003. Preliminary notes on the vertebrate fossils from the Philippines. Proceedings of the Society of Philippine Archaeologists 1, 46–62.

de Vos, J., van den Hoek Ostende, W., van den Bergh, G., 2007. Patterns in insular evolution of mammals: a key to island palaeobiogeography. In: Renema, W. (Ed.), Biogeography, Time and Place: Distributions, Barriers and Islands. Springer, Dordrecht, pp. 315–345.

Table 1

Summary of the measurements (in mm) for *Celebochoerus* upper canines referred to in this work.

Formation	Site	*n*	Mesiodistal diameter					Vestibulolingual diameter				
			Median	Mean	St dev	Min.	Max	Median	Mean	St dev	Min.	Max
Awidon Mesa (PH)	Cagayan	1	29.5	29.5	–	29.5	29.5	21.5	21.5	–	21.5	21.5
Beru subunit A (SU)	Bulu Cepo	2	40.55	40.55	13.5057	31	50.1	33	33.00	7.07107	28	38
Beru subunit A (SU)	Lonrong 1	15	41.4	39.9	5.40826	29.8	47.6	35	35.15	5.68141	25.1	46.1
Beru subunit A (SU)	Lonrong 2	5	35	36.08	4.72832	31	42	34	33.38	4.65639	27	37.8
Beru subunit A (SU)	Sompe[a]	54	30.5	31.19	5.95921	22	44	28	27.96	5.06547	20	39
Beru subunit A (SU)	Sompe 4	4	34.6	34.43	6.42981	27.2	41.3	29.55	29.6	4.16093	25.9	33.4
Beru subunit B (SU)	Beru	3	30	30.33	2.51661	28	33	27	28.33	2.30940	27	31
Beru subunit B (SU)	Lakibong 1	2	34	34	3.67696	31.4	36.6	30	30.00	4.66691	26.7	33.3
Beru subunit B (SU)	Lakibong 2	17	29.5	28.58	4.38827	18.2	34	25.1	27.26	3.92111	22.1	34.6
Beru subunit B (SU)	Padali	1	41.5	41.5	–	41.5	41.5	35.6	35.6	–	35.6	35.6
Beru subunit B (SU)	Sare Batue 2	6	33.85	33.53	5.76356	25.1	42.3	30.75	30.1	5.59964	22.1	36.3
Beru subunit B (SU)	Sare Batue 4	4	36.2	34.8	10.1987	21.1	45.7	30.35	29.25	9.12232	17.1	39.2
Tanrung (SU)	Tanrung	3	27.7	29.37	3.78594	26.7	33.7	25	25.3	3.55950	21.9	29

St dev: standard deviation; Min.: minimum; Max.: maximum.

[a] Measurements are from Hooijer (1949).

Table 2

Summary of the measurements (in mm) for *Celebochoerus* lower third molars referred to in this work.

Formation	Site	*n*	Mesiodistal diameter					Vestibulolingual diameter				
			Median	Mean	St dev	Min.	Max	Median	Mean	St dev	Min.	Max
Awidon Mesa	Cagayan	3	29.3	28.8	0.9539	27.7	29.4	14.2	13.9	0.7	13.1	14.4
Lower Beru (SU)	Bulu Cepo	3	29	29.57	2.4987	27.4	32.3	16.3	16.2	0.6557	15.5	16.8
Lower Beru (SU)	Lonrong	19	32.5	31.53	3.0665	28.1	34	16.9	17.3	1.5395	16	19
Lower Beru (SU)	Sompe[a]	18	28.4	28.75	2.2683	26	34.8	15.75	15.68	1.5859	12.9	19.1
Lower Beru (SU)	Sompe 4	2	31.8	31.37	2.2037	26.8	34.8	16.9	16.84	0.8519	15.5	19.1
Upper Beru (SU)	Lakibong 1	3	31.45	31.45	1.2021	30.6	32.3	16.45	16.45	1.0607	15.7	17.2
Upper Beru (SU)	Lakibong 2	10	29.8	29.45	1.1091	27.9	30.3	15.6	15.5	0.9092	14.3	16.5
Upper Beru (SU)	Padali	2	31	30.91	1.9855	26	34.4	16.35	16.19	1.1641	12.9	17.7
Upper Beru (SU)	Sare Batue 4	4	29.2	29.2	1.1314	28.4	30	16.8	16.8	0	16.8	16.8
Tanrung (SU)	Tanrung	1	30.7	30.7	–	30.7	30.7	16.4	16.4	–	16.4	16.4

St dev: standard deviation; Min.: minimum; Max.: maximum.
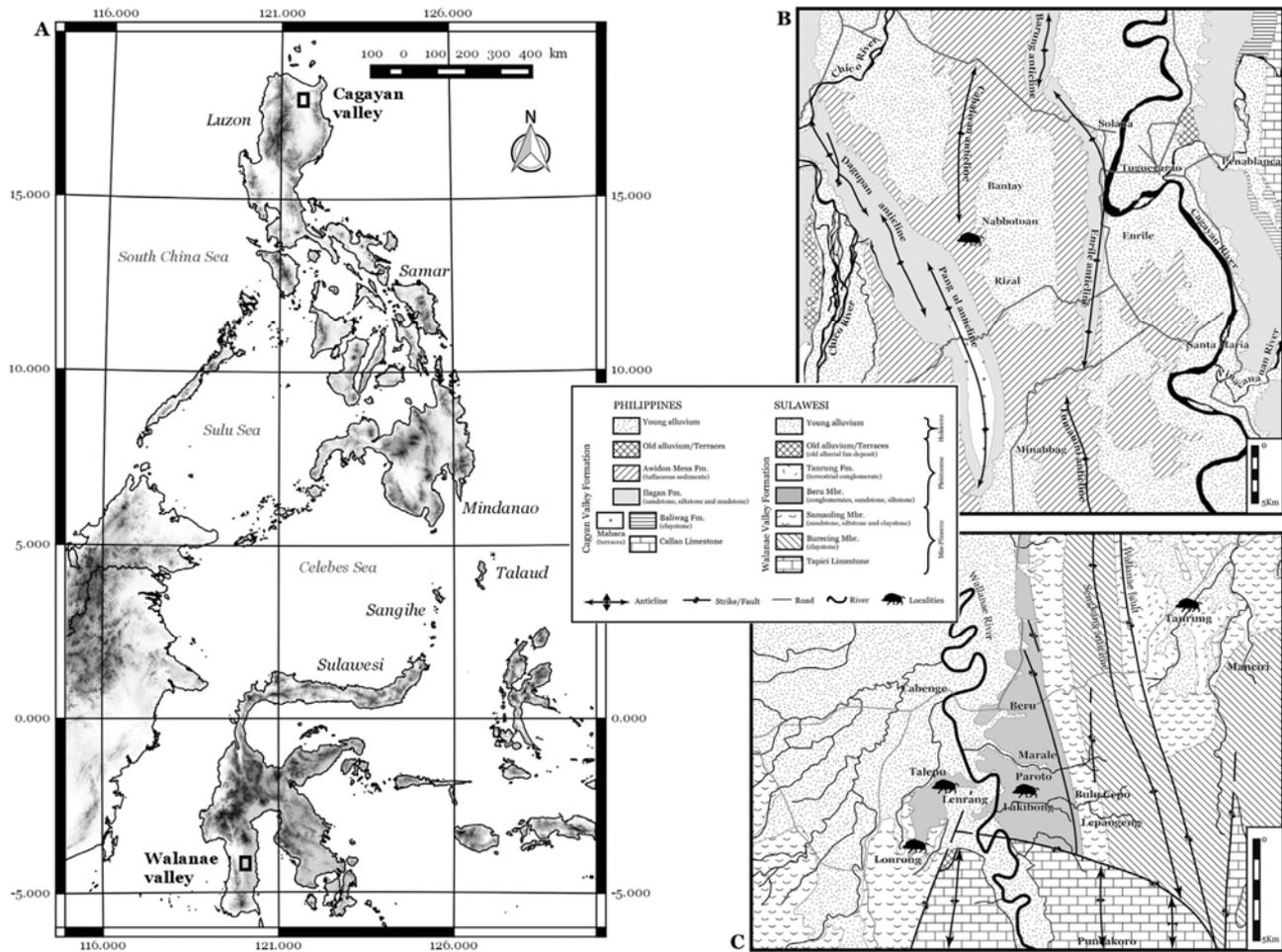
[a] Measurements are from Hooijer (1949).

Fig. 1. A. Map showing the origin of *Celebochoerus* fossils in Southeast Asia. B. Geological map of the Cagayan Valley in Luzon Island, Philippines. C. Geological map of the Walanae Valley in Sulawesi, Indonesia.
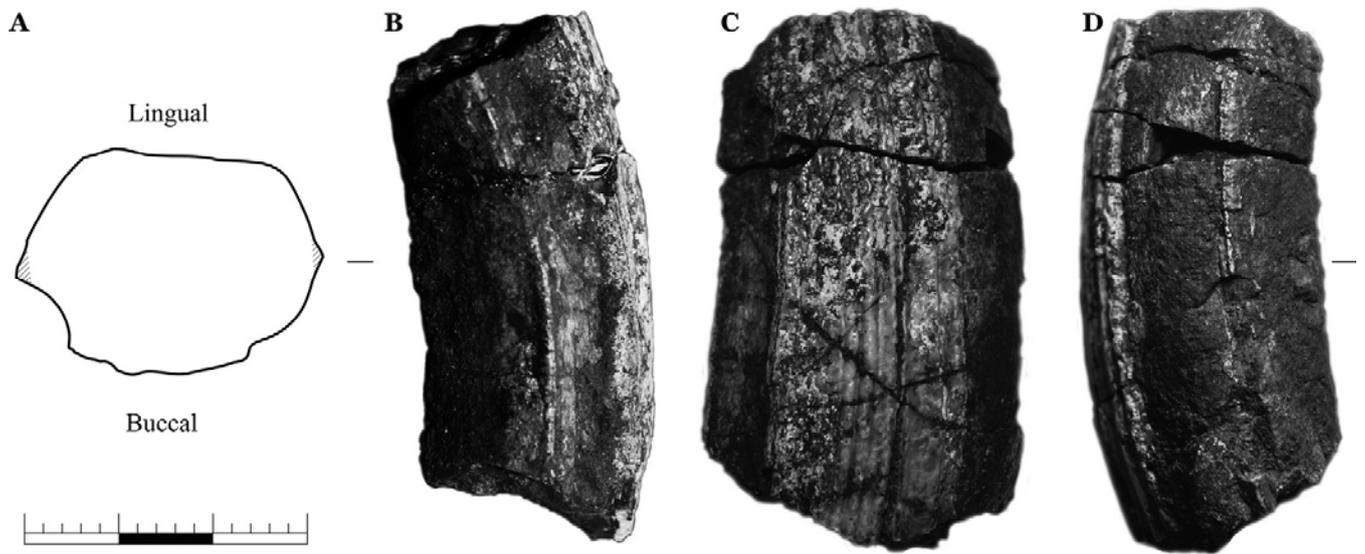
Fig. 2. *Celebochoerus cagaynensis* nov sp.: type specimen in cross-section (A), mesial (B), buccal (C), and distal (D) views. Hatches on the cross-section highlight the position of the enamel bands. Scale bar: 3 cm.
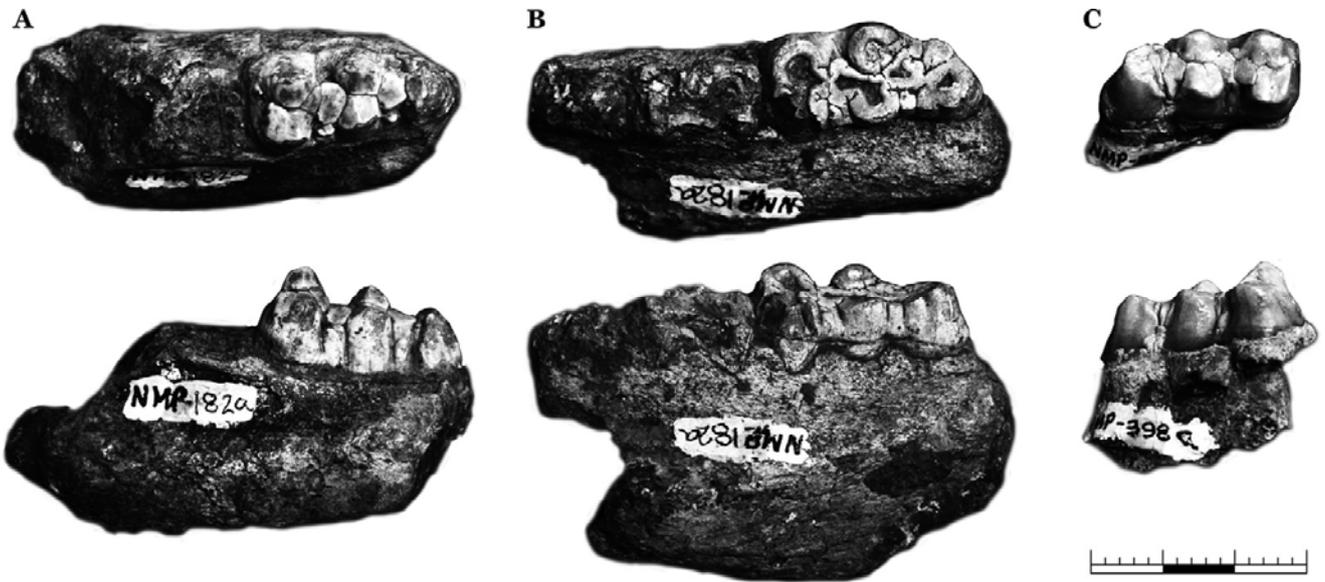
Fig. 3. *Celebochoerus cagayanensis* nov. sp.: specimens NMP 182a (A), NMP 182b (B), and NMP 398a (C) in occlusal (above) and lateral (below) views. Scale bar: 3 cm.
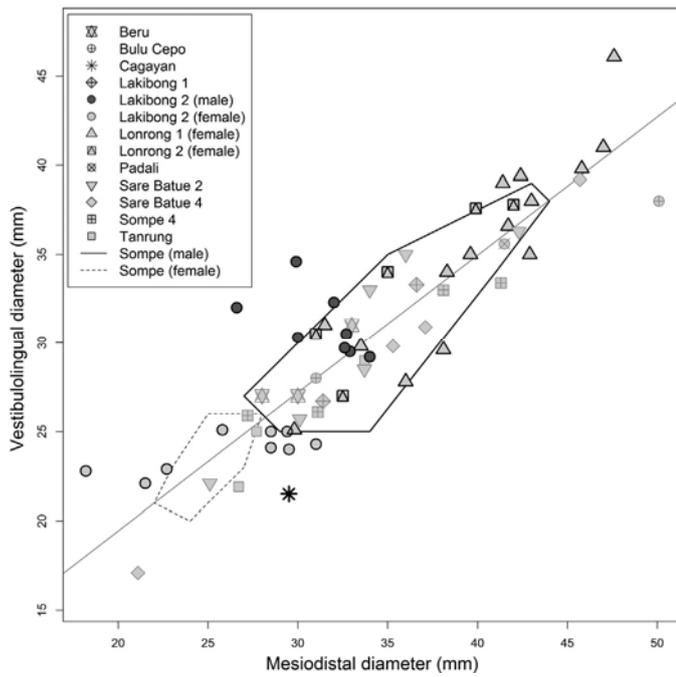
Fig. 4. Mesiodistal and vestibulolingual diameter of the *Celebochoerus* upper canines from the Philippines and Sulawesi. The convex hulls account for the dispersion of male and female specimens from Sompe (Sulawesi) measured by Hooijer (1954). We distinguish males and females only whenever a sufficiently large sample originated from a single locality.
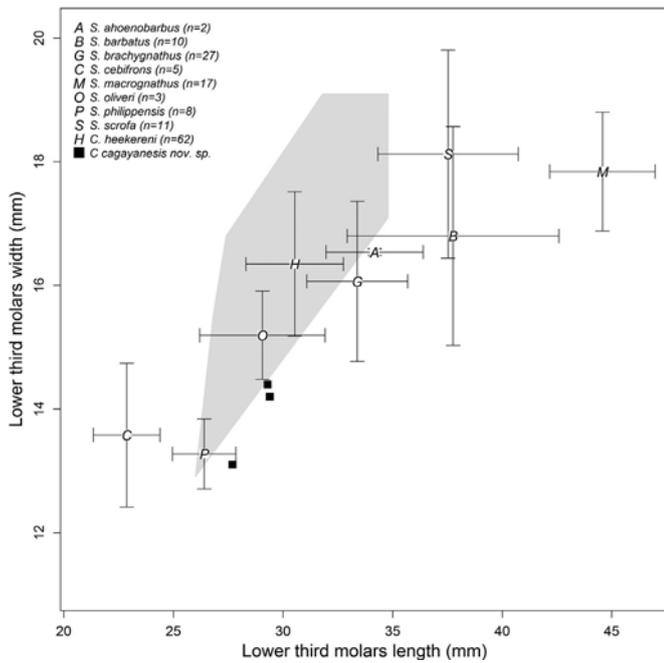
Fig. 5. Length and width of lower third molars of *Celebochoerus cagayanensis* nov sp. (black squares) compared to Island Southeast Asian fossil and extant species. The crosses represent the standard deviation around the mean. *Sus brachygnathus* and *S. macrognathus* are fossils from Java, *S. ahoenobarbus*, *S. barbatus*, *S. cebifrons* and *S. oliveri* are all extant dwarf endemic species from the Philippines. *S. scrofa* is the introduced domestic pig here measured on specimens from Island Southeast Asia. For each taxon the number of specimens is indicated within parentheses. The grey- filled convex hull accounts for the whole population of *C. heekereni*. The measurements for *C. heekereni* from Sompe are taken from Hooijer (1954).