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Aberrant growth of maxillary canine teeth in male babirusa (genus *Babyrousa*)

Croissance aberrante des dents canines maxillaires chez les mâles babirusa (genre Babyrousa*)*

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ABSTRACT

A worldwide survey of babirusa skulls curated in museum and private collections located 431 that were from adult males and had retained at least one maxillary canine tooth. Eighty-three of these skulls were identified as exhibiting aberrant maxillary canine tooth growth. Twenty-four of the skulls represented babirusa from Buru and the Sula Islands, and forty-five skulls represented babirusa from Sulawesi and the Togian Islands. The remaining series of fourteen babirusa skulls originally came from zoo animals. Fifteen skulls showed anomalous alveolar and tooth rotation in a median plane. Twenty-nine skulls had maxillary canine teeth that did not grow symmetrically towards the median plane of the cranium. Fourteen skulls showed evidence that the tips of one or both maxillary canine teeth had eroded the nasal bones. Twenty-one skulls had maxillary canine teeth that had eroded the frontal bones. The teeth of two skulls had eroded a parietal bone. One skull had two maxillary canines arising from an adjacent pair of alveoli on the left side of the cranium. Three skulls exhibited alveoli with no formed maxillary canine teeth in them. Analysis suggested that approximately 12% of the adult male babirusa in the wild experience erosion of the cranial bony tissues as a result of maxillary canine tooth growth. There was no skeletal evidence that maxillary canine teeth penetrate the eye.

RÉSUMÉ

Une enquête mondiale sur les crânes de babiroussa collectés dans des collections muséales et privées a permis de localiser 431 crânes provenant de mâles adultes ayant conservé au moins une canine maxillaire. Quatre-vingt-trois de ces crânes ont été identifiés comme présentant une croissance aberrante des canines maxillaires. Vingt-quatre des crânes

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représentaient les babiroussas des îles Buru et Sula, et quarante-cinq crânes représentaient les babiroussas des îles Sulawesi et Togian. Les séries restantes de quatorze crânes de babiroussas provenaient à l'origine d'animaux de zoo. Quinze crânes ont montré une rotation anormale alvéolaire et dentaire dans un plan médian. Vingt-neuf crânes avaient des canines maxillaires qui n'avaient pas poussé de manière symétrique autour du plan médian du crâne. Quatorze crânes ont montré que les pointes d'une ou des deux canines maxillaires avaient érodé les os nasaux. Vingt et un crânes avaient des canines maxillaires qui avaient érodé l'os frontal. Les dents de deux crânes avaient érodé un os pariétal. Un crâne avait deux canines maxillaires issues d'une paire adjacente d'alvéoles sur le côté gauche du crâne. Trois crânes présentaient des alvéoles sans canines maxillaires formées. L'analyse a suggéré qu'environ 12 % des mâles adultes babiroussas en milieu sauvage expérimentent une érosion des tissus osseux crâniens à la suite de la croissance des canines maxillaires. Il n'y avait aucune preuve squelettique de ce que les canines maxillaires pénètrent dans l'œil.

1. Introduction

One of the pigs endemic to the Indonesian islands of Buru, Sulawesi and a number of the smaller islands in their vicinity is the babirusa (genus *Babyrousa*). The unusual anatomy of the canine teeth of the adult male has long made this animal the subject of curiosity and scientific investigation [1–5]. Study of its teeth in particular has generated a better understanding of the babirusa's agonistic behaviour [6–8]. The normal growth of the open-rooted maxillary canine teeth from birth to adulthood, as recently described, involves the rotation of the maxillary canine tooth alveolus in a subcutaneous median plane to bring the tooth to point first rostrally and then progressively in a dorsal direction [9]. The tooth tip then grows out of the alveolus and pierces through the skin lateral to the nose, its curled tip pointing caudally. As it elongates the axial curvature is reduced, lifting the tip of each canine tooth along the median plane of the skull, up and over first the nasal bones and then over the frontal bone [9,10]. However, not all maxillary canine teeth follow this normal pattern. Grzimek [11] and Mohr [12] reported a male babirusa in Brookfield zoo, Chicago that had maxillary canine teeth that projected rostrally and crossed one another, left over right. McIntosh [13] illustrated part of a skull where the right maxillary canine had punctured the parietal bone. Awareness of canine maxillary tooth growth under the enhanced dietary regime of zoological collections has for a number of years prompted veterinary caution and the early trimming of canine teeth [14,15]. It was widely suggested on Buru Island in Maluku, Indonesia, recently that the maxillary teeth of the babirusa there eventually grow into the eyes of the male and to cause blindness and death [5].

The incidence of aberrant canine tooth growth in the babirusa has not been studied before. The opportunity to do so was presented by a worldwide survey of babirusa skulls curated in museum and private collections. Of these 431 were adult male and had retained at least one maxillary canine tooth. Evidence of anomalous canine tooth growth was looked for in this sample, categorised in relation to the normal pattern of tooth growth, and quantified. The results have been analysed to identify potential causes of the aberrations found and to suggest methods of amelioration.

2. Materials and methods

Eighty-three adult male babirusa skulls were identified as exhibiting aberrant maxillary canine tooth growth (Table 1). Of these 24 skulls represented babirusa from Buru and the Sula Islands, and 45 skulls represented babirusa from Sulawesi and the Togian Islands. The remaining series of 14 babirusa skulls originally came from zoo animals; based on morphometric criteria [2] and studbook data [17], it was deduced that these originated from Sulawesi Island. An additional five Sulawesi skulls showing mandibular alveolar anomalies were included in this study for discussion purposes (Table 1). The criteria for normal maxillary canine growth of the male babirusa have recently been described [10].

3. Results

The babirusa skulls exhibited a range of anomalies of maxillary canine tooth growth that could be grouped under eight headings. Some skulls featured under more than one heading.

3.1. Failure of the tooth alveolus to rotate normally

Fifteen skulls showed various amounts of reduced tooth rotation reflecting anomalous alveolar rotation in a median plane (Fig. 1). In thirteen skulls (three from Buru and the Sula Islands and ten from Sulawesi) both maxillary canine teeth were orientated more rostrally than 70 degrees with respect to the hard palate; the mean angle of rotation was 45 ± 12.4 degrees and ranged from 10 to 60 degrees. Two Sulawesi skulls each had one tooth orientated at 70 and 75 degrees respectively. The Sulawesi skull illustrated in Fig. 1A showed the lowest value for tooth rotation found. Although the external structures of the alveoli in this skull

Table 1
A list of the international reference numbers for the 83 babirusa skulls (AAM number), their Indonesian geographic origin, the museum collection where they are curated, the museum country, their registered museum specimen number and the maxillary canine anomaly noted.

AAM number	Indonesian region	Museum Collection	Country	Museum ID	Aberrant growth
AAM0004	Sula or Buru Islands	Zoological Museum Amsterdam	Netherlands	ZMA.MAM.00805	2
AAM0016	Sulawesi	Zoological Museum Amsterdam	Netherlands	ZMA.MAM.01184	1
AAM0024	Sulawesi	Zoological Museum Amsterdam	Netherlands	ZMA.MAM.02242	5
AAM0025	Sulawesi	Zool Museum Amsterdam	Netherlands	ZMA.MAM.08936	9
AAM0031	Sula Islands	Zoological Museum Amsterdam	Netherlands	ZMA.MAM.09116	2
AAM0050	Sula or Buru Islands	Zoological Museum Amsterdam	Netherlands	ZMA.MAM.25389	1
AAM0059	Sulawesi	Naturhistorisches Museum Basel	Switzerland	C.2882	2
AAM0066	Sula or Buru Islands	Naturhistorisches Museum Basel	Switzerland	C.6204	2
AAM0068	Sula or Buru Islands	Naturhistorisches Museum Basel	Switzerland	C.111.196	2
AAM0080	Sulawesi	Museum für Naturkunde, Berlin	Germany	1969	9
AAM0084	Sulawesi	Museum für Naturkunde, Berlin	Germany	8433	8
AAM0085	Sulawesi	Museum für Naturkunde, Berlin	Germany	8435	2
AAM0086	Sulawesi	Museum für Naturkunde, Berlin	Germany	8437_cran	2
AAM0091	Sula or Buru Islands	Museum für Naturkunde, Berlin	Germany	33677	4
AAM0099	Sulawesi	Museum für Naturkunde, Berlin	Germany	46526	2, 5
AAM0104	Sula or Buru Islands	Museum für Naturkunde, Berlin	Germany	64534	4
AAM0109	Sula or Buru Islands	Museum für Naturkunde, Berlin	Germany	A2620	1
AAM0137	Buru	Museum Zoologicum Bogoriense, Cibinong	Indonesia	1081	4
AAM0154	Sulawesi	Museum Zoologicum Bogoriense, Cibinong	Indonesia	6904	8
AAM0158	Buru	Museum Zoologicum Bogoriense, Cibinong	Indonesia	6908	4
AAM0195	Sulawesi	Zoologisk Museum, København	Denmark	M0321	2
AAM0198	Sulawesi	Zoologisk Museum, København	Denmark	M1433	5
AAM0203	Sula or Buru Islands	Skolen for Veterinærmedicin og Husdyrvidenskab, Københavns Universitet	Denmark	Vet2	2, 4
AAM0222	Sulawesi	Senckenberg Naturhistorische Sammlungen Dresden	Germany	3070	5
AAM0231	Sulawesi	National Museum of Scotland, Edinburgh	Scotland	NMS.Z.1878.1.4	5
AAM0246	Zoo	National Museum of Scotland, Edinburgh	Scotland	NMS.Z.1993.159.003	1
AAM0252	Zoo	National Museum of Scotland, Edinburgh	Scotland	NMS.Z.1999.185	2
AAM0253	Zoo	National Museum of Scotland, Edinburgh	Scotland	NMS.Z.1999.282.001	1
AAM0267	Zoo	National Museum of Scotland, Edinburgh	Scotland	NMS.Z.2004.161.002	2
AAM0270	Zoo	National Museum of Scotland, Edinburgh	Scotland	NMS.Z.2006.033.002	1
AAM0272	Zoo	National Museum of Scotland, Edinburgh	Scotland	NMS.Z..2006.082	2
AAM0275	Zoo	National Museum of Scotland, Edinburgh	Scotland	NMS.Z.2008.026. Morvell	2
AAM0283	Sulawesi	Naturmuseum Senckenberg, Frankfurt Am Main	Germany	423	2
AAM0287	Buru	Naturmuseum Senckenberg, Frankfurt Am Main	Germany	427	4
AAM0288	Buru	Naturmuseum Senckenberg, Frankfurt Am Main	Germany	429	5
AAM0290	Sulawesi	Naturmuseum Senckenberg, Frankfurt Am Main	Germany	1588	6
AAM0293	Zoo	Naturmuseum Senckenberg, Frankfurt Am Main	Germany	5951	2
AAM0317	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.938	2
AAM0319	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.940	2
AAM0323	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.944	5
AAM0326	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.947	2, 9
AAM0333	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.954	5
AAM0334	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.955	5
AAM0336	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.957	1
AAM0337	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.958	6
AAM0339	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.960	9
AAM0340	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.961	2
AAM0347	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.968	2
AAM0357	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.978	1, 9
AAM0365	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.986	5
AAM0369	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.990	5
AAM0370	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.991	9
AAM0372	Sulawesi	Museum of Comparative Zoology - Harvard University	USA	BOM1910	5
AAM0374	Sulawesi	Museum of Comparative Zoology - Harvard University	USA	BOM1912	9
AAM0383	Sulawesi	Museum of Comparative Zoology - Harvard University	USA	MCZ46401	5
AAM0385	Sulawesi	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.00375	5, 9
AAM0386	Sulawesi	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.00992	8
AAM0396	Buru	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.28805	5, 7
AAM0407	Sula or Buru Islands	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.28819	4
AAM0408	Sulawesi	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.43508	4
AAM0412	Sulawesi	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.28802	2
AAM0413	Sulawesi	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.00089a	1
AAM0429	Sulawesi	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.43503[nonum06]	5
AAM0450	Sula Islands	Natural History Museum, London	England	19.11.23.04	4
AAM0461	Sulawesi	Natural History Museum, London	England	0.3.30.19	2
AAM0463	Sulawesi	Natural History Museum, London	England	9.11.30.1	2
AAM0466	Sula Islands	Natural History Museum, London	England	19.11.23.08	3, 4

Table 1 (*Continued*)

AAM number	Indonesian region	Museum Collection	Country	Museum ID	Aberrant growth
AAM0473	Sula or Buru Islands	Natural History Museum, London	England	67.4.12.221	2
AAM0507	Sula Islands	Zoologische Staatssammlung München	Germany	ZSM1908_2729	2
AAM0514	Sula or Buru Islands	Zoologische Staatssammlung München	Germany	ZSM1949_1414	4
AAM0526	Sulawesi	American Museum of Natural History, New York	USA	69415	1
AAM0527	Buru	American Museum of Natural History, New York	USA	90363	5
AAM0543	Togean Islands	American Museum of Natural History, New York	USA	153408	4
AAM0561	Sulawesi	Lee Kong Chian Natural History Museum	Singapore	ZRC.4.1953	2
AAM0588	Sulawesi	Naturhistoriska Riksmuseet, Stockholm	Sweden	A585922	2
AAM0600	Zoo	Kibun Binatang Surabaya	Indonesia	D.BB.Rusa13_10_92	5
AAM0601	Zoo	Kibun Binatang Surabaya	Indonesia	19_8_98	1
AAM0603	Zoo	Kibun Binatang Surabaya	Indonesia	5_6_89	5
AAM0605	Zoo	Kibun Binatang Surabaya	Indonesia	Pf605	1
AAM0607	Zoo	Kibun Binatang Surabaya	Indonesia	19_8_88	1
AAM0612	Sulawesi	Naturhistorisches Museum Wien	Austria	1493	4
AAM0634	Zoo	National Museum of Natural History, Washington	USA	283108	1
AAM0674	Sulawesi	Zoology museum, University of Aberdeen	Scotland	RN20523	5
AAM0734	Sula or Buru Islands	Muséum national d'histoire naturelle, Paris	France	MNHN-ZM-AC 1880-618E	1
AAM0742	Sula or Buru Islands	Muséum national d'histoire naturelle, Paris	France	MNHN-ZM-AC 1993-4617	4
AAM0763	Sulawesi	De faculteit Diergeneeskunde, Universiteit Utrecht	Netherlands	TAG_277	2
AAM1774	Sula or Buru Islands	Muséum des sciences naturelles, Bruxelles	Belgium	3712	5
AAM1794	Sulawesi	Natural History Museum at the University of Oslo	Norway	M7237	5
AAM0004	Sula or Buru Islands	Zoological Museum Amsterdam	Netherlands	ZMA.MAM.00805	2
AAM0016	Sulawesi	Zoological Museum Amsterdam	Netherlands	ZMA.MAM.01184	1
AAM0024	Sulawesi	Zoological Museum Amsterdam	Netherlands	ZMA.MAM.02242	5
AAM0025	Sulawesi	Zool Museum Amsterdam	Netherlands	ZMA.MAM.08936	9
AAM0031	Sula Islands	Zoological Museum Amsterdam	Netherlands	ZMA.MAM.09116	2
AAM0050	Sula or Buru Islands	Zoological Museum Amsterdam	Netherlands	ZMA.MAM.25389	1
AAM0059	Sulawesi	Naturhistorisches Museum Basel	Switzerland	C.2882	2
AAM0066	Sula or Buru Islands	Naturhistorisches Museum Basel	Switzerland	C.6204	2
AAM0068	Sula or Buru Islands	Naturhistorisches Museum Basel	Switzerland	C.111.196	2
AAM0080	Sulawesi	Museum für Naturkunde, Berlin	Germany	1969	9
AAM0084	Sulawesi	Museum für Naturkunde, Berlin	Germany	8433	8
AAM0085	Sulawesi	Museum für Naturkunde, Berlin	Germany	8435	2
AAM0086	Sulawesi	Museum für Naturkunde, Berlin	Germany	8437_cran	2
AAM0091	Sula or Buru Islands	Museum für Naturkunde, Berlin	Germany	33677	4
AAM0099	Sulawesi	Museum für Naturkunde, Berlin	Germany	46526	2, 5
AAM0104	Sula or Buru Islands	Museum für Naturkunde, Berlin	Germany	64534	4
AAM0109	Sula or Buru Islands	Museum für Naturkunde, Berlin	Germany	A2620	1
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AAM0154	Sulawesi	Museum Zoologicum Bogoriense, Cibinong	Indonesia	6904	8
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AAM0195	Sulawesi	Zoologisk Museum, København	Denmark	M0321	2
AAM0198	Sulawesi	Zoologisk Museum, København	Denmark	M1433	5
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AAM0222	Sulawesi	Senckenberg Naturhistorische Sammlungen Dresden	Germany	3070	5
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AAM0253	Zoo	National Museum of Scotland, Edinburgh	Scotland	NMS.Z.1999.282.001	1
AAM0267	Zoo	National Museum of Scotland, Edinburgh	Scotland	NMS.Z.2004.161.002	2
AAM0270	Zoo	National Museum of Scotland, Edinburgh	Scotland	NMS.Z.2006.033.002	1
AAM0272	Zoo	National Museum of Scotland, Edinburgh	Scotland	NMS.Z..2006.082	2
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AAM0288	Buru	Naturmuseum Senckenberg, Frankfurt Am Main	Germany	429	5
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AAM0293	Zoo	Naturmuseum Senckenberg, Frankfurt Am Main	Germany	5951	2
AAM0317	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.938	2
AAM0319	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.940	2
AAM0323	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.944	5
AAM0326	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.947	2, 9
AAM0333	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.954	5
AAM0334	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.955	5
AAM0336	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.957	1
AAM0337	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.958	6
AAM0339	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.960	9
AAM0340	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.961	2
AAM0347	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.968	2

Table 1 (*Continued*)

AAM number	Indonesian region	Museum Collection	Country	Museum ID	Aberrant growth
AAM0357	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.978	1, 9
AAM0365	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.986	5
AAM0369	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.990	5
AAM0370	Sulawesi	Göteborgs naturhistoriska museum, Göteborg	Sweden	17.991	9
AAM0372	Sulawesi	Museum of Comparative Zoology - Harvard University	USA	BOM1910	5
AAM0374	Sulawesi	Museum of Comparative Zoology - Harvard University	USA	BOM1912	9
AAM0383	Sulawesi	Museum of Comparative Zoology - Harvard University	USA	MCZ46401	5
AAM0385	Sulawesi	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.00375	5, 9
AAM0386	Sulawesi	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.00992	8
AAM0396	Buru	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.28805	5, 7
AAM0407	Sula or Buru Islands	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.28819	4
AAM0408	Sulawesi	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.43508	4
AAM0412	Sulawesi	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.28802	2
AAM0413	Sulawesi	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.00089a	1
AAM0429	Sulawesi	Naturalis Biodiversity Center, Leiden	Netherlands	RMNH.MAM.43503 [nonum06]	5
AAM0450	Sula Islands	Natural History Museum, London	England	19.11.23.04	4
AAM0461	Sulawesi	Natural History Museum, London	England	0.3.30.19	2
AAM0463	Sulawesi	Natural History Museum, London	England	9.11.30.1	2
AAM0466	Sula Islands	Natural History Museum, London	England	19.11.23.08	3, 4
AAM0473	Sula or Buru Islands	Natural History Museum, London	England	67.4.12.221	2
AAM0507	Sula Islands	Zoologische Staatssammlung München	Germany	ZSM1908_2729	2
AAM0514	Sula or Buru Islands	Zoologische Staatssammlung München	Germany	ZSM1949_1414	4
AAM0526	Sulawesi	American Museum of Natural History, New York	USA	69415	1
AAM0527	Buru	American Museum of Natural History, New York	USA	90363	5
AAM0543	Togean Islands	American Museum of Natural History, New York	USA	153408	4
AAM0561	Sulawesi	Lee Kong Chian Natural History Museum	Singapore	ZRC.4.1953	2
AAM0588	Sulawesi	Naturhistoriska Riksmuseet, Stockholm	Sweden	A585922	2
AAM0600	Zoo	Kibun Binatang Surabaya	Indonesia	D.BB.Rusa13_10_92	5
AAM0601	Zoo	Kibun Binatang Surabaya	Indonesia	19_8_98	1
AAM0603	Zoo	Kibun Binatang Surabaya	Indonesia	5_6_89	5
AAM0605	Zoo	Kibun Binatang Surabaya	Indonesia	Pf605	1
AAM0607	Zoo	Kibun Binatang Surabaya	Indonesia	19_8_88	1
AAM0612	Sulawesi	Naturhistorisches Museum Wien	Austria	1493	4
AAM0634	Zoo	National Museum of Natural History, Washington	USA	283108	1
AAM0674	Sulawesi	Zoology museum, University of Aberdeen	Scotland	RN20523	5
AAM0734	Sula or Buru Islands	Muséum national d'histoire naturelle, Paris	France	MNHN-ZM-AC 1880-618E	1
AAM0742	Sula or Buru Islands	Muséum national d'histoire naturelle, Paris	France	MNHN-ZM-AC 1993-4617	4
AAM0763	Sulawesi	De faculteit Diergeneeskunde, Universiteit Utrecht	Netherlands	TAG_277	2
AAM1774	Sula or Buru Islands	Muséum des sciences naturelles, Bruxelles	Belgium	3712	5
AAM1794	Sulawesi	Natural History Museum at the University of Oslo	Norway	M7237	5

1: reduced alveolar rotation; 2: aberrant angle to median plane; 3: failed to penetrate skin; 4: erosion of nasal bone; 5: erosion of frontal bone; 6: erosion of parietal bone; 7: paired maxillary teeth; 8: failed tooth growth; 9: mandibular canine apex erosion of bone.

were orientated at approximately 45 degrees to the hard palate, the angles of curvature of the teeth within the alveoli were orientated rostro-ventrally. In another skull (AAM0050, from Buru or the Sula Islands), the right canine grew with a caudally orientated curvature, even though the alveolus was orientated at 10 degrees rostrally with respect to the hard palate. The flattened bony bracket along the caudal edge of the alveolus of these skulls appeared somewhat reduced in size (Fig. 1B).

3.2. *Anomalous alignment of the tooth with the median plane of the cranium*

There were 29 skulls in which one or both maxillary canine teeth did not grow (more or less) symmetrically towards the median plane of the cranium (Fig. 2). In most cases [16] the left canine tooth grew to lie over the right side of the skull (Fig. 2A); five of these skulls were from Buru or the Sula Islands and 11 from Sulawesi. In eight cases the teeth crossed one another; one from the Sula Islands and seven came from Sulawesi. In four cases the right canine tooth grew over to the left side of the face; one from Buru or the Sula Islands and three skulls were from Sulawesi. On one occasion (Sulawesi skull) the pattern of growth taken by the right maxillary canine tooth was more complex (Fig. 2B).

3.3. *Failure of the tooth to erupt through the skin*

In one skull from the Sula Islands the tight, curve-linear shape and the white superficial appearance of the left maxillary canine tooth indicated that it had not passed rostrally through the skin during its growth (Fig. 3). The curved shaft of the tooth projected rostrally, and was ridged along its caudal border. The tip of the tooth had penetrated the left nasal bone and grown into the nasal cavity. The open apex of the tooth had grown caudally into the maxilla. There was no alveolar bone ventral, rostral, lateral and medial to the tooth. Some alveolar bone, largely comprising the flattened caudally facing bracket, was present around the tooth's open apex and adjacent to the

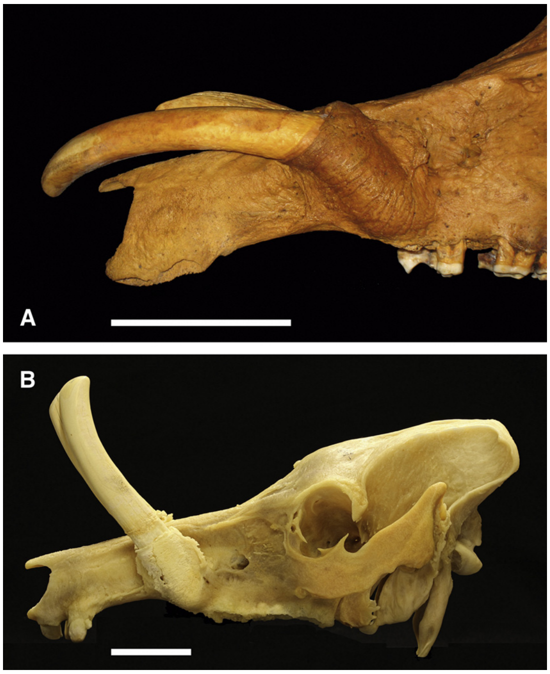

Fig. 1. A. Left lateral view of a babirusa skull (AAM0605) from an Indonesian zoo (and originating from Sulawesi) illustrating failure of the maxillary canine tooth alveolus to rotate normally and showing the orientation of the growth of these teeth to aberrantly point rostroventrally. Note that the tips of the teeth have been cut off for husbandry reasons. B. Left lateral view of a babirusa skull (AAM0253) from a European zoo (originating from Sulawesi) illustrating incomplete rotation of the maxillary canine tooth alveolus. Note that the tips of the teeth have been cut off for husbandry reasons (scale = 50 mm).

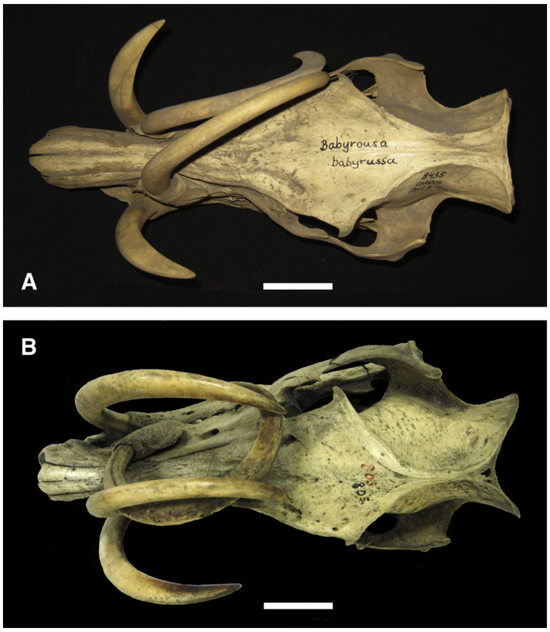

Fig. 2. A. Dorsal view of a Sulawesi babirusa skull (AAM0085) illustrating growth of both maxillary canine teeth to the right side of the head rather than to the median plane. B. Dorsal view of the skull (AAM0004) of a babirusa from Buru or the Sula Islands showing a normally grown left maxillary canine tooth and an aberrantly grown right maxillary canine tooth (scale = 50 mm).

Fig. 3. Left lateral view of a babirusa skull (AAM0466) from the Sula Islands illustrating a maxillary canine tooth tightly curled and inserting its tip through the left nasal bone into the nasal cavity. Note its bony alveolar support is restricted to the caudal surface, which shows corrugations (scale = 50 mm).

caudal edge of the tooth. The right canine tooth had grown normally to a length of 85 mm above the skin (Fig. 3).

3.4. *Canine tooth erosion of the nasal bones*

Fourteen skulls showed evidence that the tips of one or both maxillary canine teeth had eroded the nasal bones (Fig. 4). Eleven of these skulls were from Buru or the Sula Islands, and three were from Sulawesi. On six occasions, five being skulls from Buru, the tip of the tooth had penetrated the nasal bone and entered the nasal cavity (Fig. 4). The open apex of the tooth that had punctured the nasal bone appeared to have also extended the supporting alveolus caudally and in three cases eroded the integrity of the caudo-ventral surfaces of the alveolus (Fig. 4A). Those canine teeth that had not penetrated the nasal bones appeared to have normal alveoli.

3.5. *Canine tooth erosion of the frontal bones*

There were 22 skulls in which the maxillary canine teeth had eroded the frontal bones; four were from Buru and the Sula Islands and 18 were from Sulawesi and the Togian Islands. On 12 occasions the tip of the tooth had penetrated the bone and entered the frontal sinuses (Fig. 5). Three of these skulls were from Buru or the Sula Islands, and nine were from Sulawesi or the Togian Islands. On one occasion the damage was caused by the tooth on the right side of the skull reaching over the face to insert into the left frontal bone. In all cases the alveoli appeared to be normal.

3.6. *Canine tooth erosion of the parietal bones*

There were two skulls from Sulawesi where one of their maxillary canine teeth had eroded a parietal bone.

3.7. *Supernumerary maxillary canine tooth*

One skull from Buru Island had two maxillary canines arising from an adjacent pair of alveoli on the left side of

Fig. 4. A. Left lateral view of the skull (AAM0091) of a babirusa from Buru or the Sula Islands in which the left maxillary canine tooth has eroded and penetrated the left nasal bone. Note the disruption of the rostral aspect of the alveolus. Note also the ventro-caudal growth and exposure of the apex of the tooth. B. Dorsal view of the cranium (AAM0137) of a relatively young adult male babirusa from Buru demonstrating the erosion and penetration of the bones at the naso-frontal suture (scale = 50 mm).

the cranium (Fig. 6). The more rostral tooth was larger than caudo-lateral tooth (Fig. 6A), and the oval diameters of its alveolus were correspondingly larger. The external lengths of the two adjacent alveoli were similar (Fig. 6B). One maxillary canine tooth arose from the right alveolus (Fig. 6A). It was of approximately the same size as the more rostral tooth on the left side of the cranium. The tips of all three maxillary canine teeth had broken, and one had eroded and penetrated the right frontal bone (Fig. 6A).

3.8. Absence of maxillary canine tooth

Three Sulawesi skulls exhibited alveoli (two right, one left) with no formed maxillary canine teeth in them. Each alveolus was short in vertical length, appeared to have rotated normally, had an apparently normal, caudally orientated flattened bony bracket on its caudal surface, and a smaller cranial bracket. Each alveolus was somewhat flattened latero-medially. In each case the rostrally orientated remains of the alveolar lumen was filled with spongy bony.

No babirusa skull exhibited a maxillary canine tooth penetrating the eye socket.

4. Discussion

This is the first detailed analysis of aberrations in the growth of maxillary canine teeth growth in the male

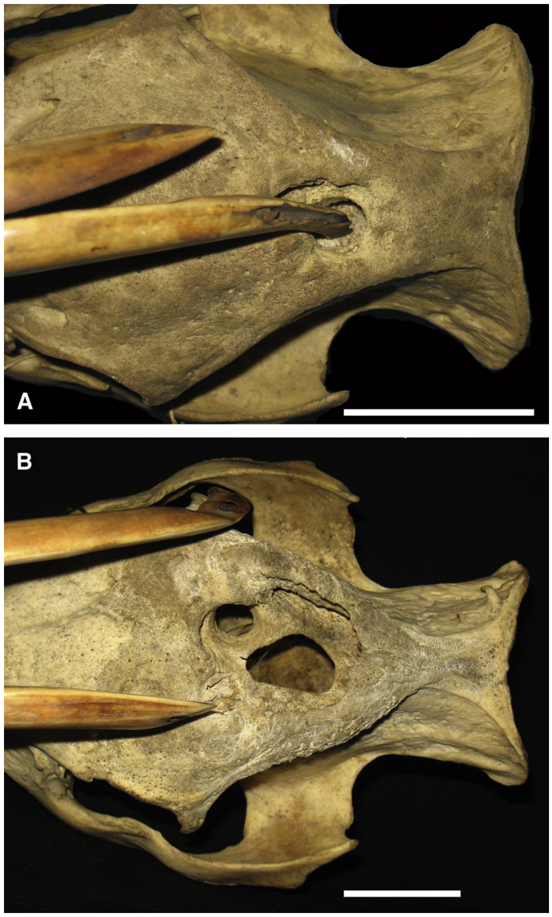

Fig. 5. A. Dorsal view of the cranium (AAM0231) of a Sulawesi babirusa illustrating the erosion of the frontal-parietal suture area and the penetration by the left maxillary canine tooth into the frontal sinuses. Note the area of superficial bone erosion around the tooth, and the size and shape of the puncture relative to the size of the tooth. B. Dorsal view of the cranium (AAM0674) of a Sulawesi babirusa illustrating the extensive erosion of the left and right frontal bones and two of the three penetrations into the frontal sinuses. There was no penetration of the cranial cavity (scale = 50 mm).

babirusa. It draws on the evidence contained in skeletal tissues gathered, stored and curated in museum collections around the world. These skulls serve as a conserved sample of the range of tooth problems to be found naturally in these animals.

A number of skulls variously showed the effect on maxillary canine growth of a failure by the alveolus to rotate into its normal position [9]. These represented a relatively small number of the aberrant skulls identified (18.1%) and only 3.5% of the 431 skulls surveyed. The underlying cause of this anomaly remains uncertain. Physical resistance to rotation may be hypothesized, but there was no structural evidence present that could be interpreted as giving support to this notion. It had been suggested that normally the alveolus was slowly "pulled" into position by fascia associated with the growth of the skull during juvenile development [9]; the sutures of the skull are major sites of bone expansion during postnatal

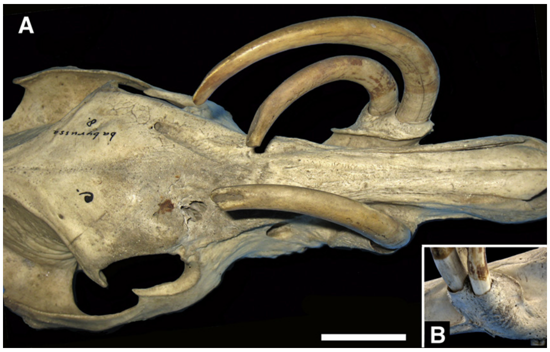

Fig. 6. A. Dorsal view of the cranium (AAM0396) of a Buru Island babirusa with two maxillary canine teeth on the left and one maxillary canine tooth on the right side of the cranium. Each canine tooth has an alveolus. Note the erosion of the right frontal bone. B. Left lateral view of the alveoli (AAM0396) on the left of the cranium illustrating their approximately similar lengths and the single caudal flattened, bony bracket.

craniofacial growth [18,19]. In almost all, fourteen, of the cases the relatively small size of the caudal bracket on the alveolus might indicate supportive evidence. However, in one of the other skulls (Fig. 1A) the relatively large caudal alveolar bracket would appear not to be consistent with this possibility. The partial rotation of the alveolus initially suggested the possibility of traumatic interference with this hypothesized mechanism. However, the bilateral failure of rotation seen in ten of the skulls would appear to argue against this possibility.

One of the zoo specimens in the present study (AAM0605) together with another one published by Grzimek [11] and Mohr [12] illustrated an additional component of this anomaly. The alveolus pointed partially rostrally, but the canine tooth grew rostro-ventrally (Fig. 1A). This suggested that one component playing a role in the growth of the tooth might be the post-alveolar weight of the canine tooth itself. Perhaps in the relatively extreme situation of rostrally orientated teeth there is enough gravitational leverage of the erupted tooth to have an effect on the odontoblasts in the apical region of the alveolus; clearly more dentine tissue was laid down linearly on the dorsal side of the tooth than on the ventral side and so the tooth grew ventrally (Fig. 1A). Recent studies have shown that microgravity and applied pressures contribute to the bioengineering of tooth tissue [20,21].

Abnormal alignment of the maxillary canine teeth with respect to the median plane was recognized as such in 29 skulls. These represented 34.9% of the anomalous sample, and 6.7% of all the skulls observed. Various suggestions would seem to indicate explanations for the range of variation seen. Failure of the maxillary canine teeth to meet appropriately in the median plane may well have resulted in teeth crossing over one another. A small wear pattern has been reported on the adjacent medial surfaces of normally grown maxillary canine teeth [8]. Trauma on one side may have led to partial disorientation of one tooth (Fig. 2A). It was earlier suggested that because Babirusa rub their canine teeth against the walls of their pens, and even the legs of their keepers they thereby modify the direction of growth of the teeth [22,23].

Initially it was puzzling to explain the circumstances that brought about the sinuous path taken by the right maxillary canine tooth in Fig. 2B. However, one possible suggestion was that the right canine tooth grew under the growth path of the left canine tooth and that pressure exerted on the former's lateral surface proximally and distally induced the growth pattern shown (Fig. 2B). Its alveolus appeared normal externally.

Thirty-six of the skulls showed tooth-induced erosion of the bones of the cranium, and this anomaly represented 8.3% of the 431 adult male babirusa skulls examined. The skulls that had maxillary canine teeth penetrating the nasal bones were mainly from Buru and the Sula Islands (11 of 14), whereas the skulls with teeth penetrating the frontal and parietal bones were mainly from Sulawesi and the Togian Islands (18 of 22). These differences reflected the geographically based difference in patterns of normal growth of the maxillary canine teeth [10]. An additional seventeen skulls (3.9%), all from Sulawesi, had maxillary canine teeth that showed anatomical signs of potential future damage to the cranial bones, interrupted by having been trapped and killed by local people. Comparable images, of maxillary canine teeth tips resting on the forehead skin of babirusa, were seen in video recordings made in North Sulawesi [8,24] (Macdonald, unpublished). Thus, when taken together these data suggested that approximately 12% of the adult male babirusa in the wild would experience erosion of the cranial bony tissues as a result of maxillary canine tooth growth.

This incidence of damage to the nasal, frontal and parietal bones of the adult male babirusa skull by the growing maxillary canine teeth was greater than expected. The published literature had only made mention of two examples [13,25,26]. One of these, the rotation of the maxillary tooth illustrated in Fig. 3, was likely to have been caused by the failure of the tooth to penetrate the skin. It is unclear if this was due to insufficient hardness of the tip. The tip of the juvenile *Sus scrofa* maxillary canine tooth is initially covered in enamel [27], but it is not yet known if this is the case in babirusa [10]. An alternative suggestion was that "over rotation" of the alveolus may have occurred such that the tip of the tooth was carried past the appropriate angle to pierce the skin. However, the appearance of the remaining elements of the alveolus would seem to argue against this possibility (Fig. 3). Another hypothesis was that there had been greater resistance of the skin to being punctured. Nevertheless, the contralateral tooth grew normally. The observation that the tip of the left canine tooth penetrated and was then mechanically caught in the left nasal bone, and yet continued to grow in a curve, supported the hypothesis that there was some form of pressure/resistance feedback mechanism to the tooth growth cell multiplication region within the alveolus [10]. The absence of skin or bone pressure on the tip of the contralateral tooth seemed to have enabled a more linear pattern of growth as the normal result.

The caudal direction of growth shown by the open apex of the left maxillary canine tooth (Fig. 3) was comparable

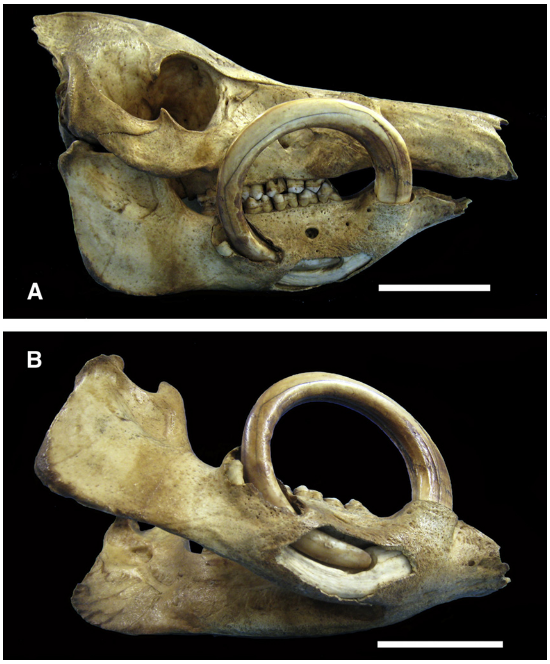

Fig. 7. A. Right lateral view of the skull (AAM0385) of a Sulawesi babirusa illustrating the curved path taken by the growing mandibular canine tooth. Note the penetration by the tooth apex of the bony mandibular tissue caudal to the encircling shaft of the tooth. B. Right ventro-lateral view of the mandible (AAM0385) of the same Sulawesi babirusa with a window cut into the bony mandibular tissue to reveal the path taken by the tip of the tooth through the bone and into the shaft of the tooth itself. The apex of the tooth has grown through the lateral bony tissue of the mandible and lies caudal to the curved shaft of the tooth (scale = 50 mm).

to that shown by the aberrant growth of a babirusa mandibular canine tooth reported by Meyer [25]; he drew attention to a right canine tooth that had grown in a complete circle and re-entered the jaw (Fig. 7A). It appeared to have had a tight curve-linear growth pattern from early in its development. This pattern had continued through adulthood with the tip of the tooth remaining inside the oral cavity, where it first grew dorsally, then caudally before pointing ventrally, lateral to itself. Within the jaw the tooth tip had overlapped and insinuated itself into its own tooth shaft. The growth of the tooth, at its open apex, appeared to have forced that end of the tooth to move caudally through the bony alveolar tissue of the mandible and had caused it to partially erupt from the lateral surface of the mandible (Fig. 7B).

Ten additional examples of caudal growth of the open apex of the mandibular canine tooth through the mandibular periosteum were noted in the present study (Table 1); in each case that part of the tooth had eroded through the supporting bony tissue of the lateral surface of the mandible and partially or completely entered the overlying connective tissue space. These findings would seem to support the suggestion that the physical resistance to growth of the tooth in the normal rostral-dorsal direction had been greater than that which normally retained the open apex of the tooth within the cortex of the mandible, and had thus led to its extension caudo-dorsally.

Caudal growth of the canine tooth apex has been recorded in the narwhal during normal growth [28].

Bilateral anomalous circular growth of the mandibular canine teeth of *Sus scrofa*, back into and through the mandible, has been described by Cheselden [29] and Miles [26]. Similarly overgrown canine teeth have been deliberately produced by human removal of the upper canines in young domesticated male pigs [30]. Anomalous growth of a mandibular canine tooth has also been recorded in an Arizona peccary (*Pecari tajacu*) in which the left canine tooth was described as having split into three parts [31]. Re-analysis by Miles and Grigson [32] led them to conclude that there had been two tooth germs, the apexes of which had fused. The illustration suggested that the tooth root had rotated on its axis and its "combined apex" had become seated ventrally in the mandible rather than caudally [31]. The two unequal parts of this combined tooth curved rostrally and appear to have pierced ventrally out of the mandible; one additional malformed part did rise dorsally. Recent reviews of the human and animal literature suggest that many of the mechanisms controlling normal tooth growth remain to be elucidated [33–35].

It has been recognized for some time that the skulls of babirusa from Buru and the Sula islands are smaller than those from Sulawesi [2,12]. It was also recognized that the canine teeth of babirusa from Buru and the Sula islands tended to be slenderer than those from Sulawesi, which are larger and longer in size [2]. This enlarged size together with their pattern of angular growth [10] seemed to explain why the maxillary canine teeth of Sulawesi skulls generally reached over the nasal bones and eroded and penetrated some of the skulls more caudally than those from Buru and the Sula Islands.

A number of the skulls showed very well-defined penetrations of the skull that closely matched the sizes of the penetrating teeth (Figs. 3 and 4). Other skulls had large areas of bony erosion around penetration sites that were much larger than the diameter of the causal tooth (Figs. 5A and B). The latter suggested that the animal had experienced a relatively long period of pressure on the cranial tissues from its canine tooth. The size of the hole also indicated that the animal had rubbed its head and the tooth for a long period of time causing the latter to create extensive destruction of specific areas of the cranium. Normally the adult male rubbed the side of his face against small diameter trees and saplings to deposit olfactory secretions from the glands in his eye sockets and from its mouth [5,6]. He also ploughed his nose and face into soft and wet substrate [8,36] as well as rubbed the side of his face against stones and the sides of wallows [37]. These caused wear of the maxillary canine teeth particularly on their lateral side towards the tips of the teeth [8]. Often this wear was sufficient to cause the teeth to thin and break, resulting in a sharp point or flat edge (Fig. 2A, Fig. 4, Fig. 6A). The erosion of the frontal and parietal bones would appear to have occurred following such breakage. The relatively large amount of mobility of the maxillary canine tooth within its alveolus was likely to be the cause of the large area of bony erosion. The maxillary alveolus provided about 50 mm of support, but the exposed tooth could be over 400 mm long; 432 mm and 425 mm are the two longest measurements of maxillary canine teeth recorded from Sulawesi babirusa [38]. By way of contrast, the mandibular alveolus provided substantially better support, by quite tightly holding about 50% of the length of the mandibular canine tooth.

Supernumerary maxillary canine teeth would appear to be rare in babirusa (Fig. 6). We did not investigate whether other, non-canine supernumerary teeth were present in the skulls under investigation. In a smaller survey of babirusa, none were reported by Miles and Grigson [32], although they did comment upon and depict a domestic pig (*Sus scrofa*) with two mandibular canine teeth on each side. They also indicated that there have been a number of descriptions of bilateral paired tusks (incisors) in African elephants (*Loxodonta africana*). Two walrus (*Odobaenus rosmarus*) have been found with supernumerary maxillary canine teeth on one side of the skull [39], and an instance of duplication of both maxillary canine teeth has also been reported [40].

Clearly the age of the babirusa was likely to be an important factor in the incidence of those tooth aberrations where erosion of the frontal and parietal bones had occurred. As the adult male babirusa grows older the length of the maxillary canine teeth grow longer. Methods are available for determining the ages of wild bushpig (*Potamochoerus larvatus*) [41], Eurasian wild pig (*Sus scrofa*) [42], and warthog (*Phacochoerus africanus*) [43]. However, there are as yet no clearly defined ways of aging babirusa from the wild. The presence of babirusa of Sulawesi origin in international zoological collections offers the opportunity to monitor and describe age changes in canine tooth growth [17]. It is recognized that there will be some form of impact of zoo diet, veterinary care and general animal management on tooth growth (Fig. 1B). It is also well known that most animal species in zoological collections tend to live longer than those in the wild [44]. Currently, male babirusa in zoos are living over 12 years (when fecundity starts to markedly decline) up to 19 years of age [17]. Veterinary awareness of the possibility that the maxillary canine might grow into the forehead of the animal, and mindfulness of the brittle nature of the babirusa's canine teeth [12], has for many years led to precautionary trimming of those teeth in zoos (Fig. 1B). Modern veterinary anaesthetic procedures facilitate such procedures and as a result, the maxillary canine teeth are cut as a precaution in many zoological collections [14,15]. Failure of canine teeth to erupt through the skin (Fig. 3) has occurred in zoological collections, and has been surgically treated successfully. Treatment of injured canine teeth has also been effective [15,44]. Although somewhat flattened and filled with spongy bone, the three maxillary canine alveoli that were found empty of teeth had dorsal dimensions and structure that suggested each one had formerly accommodated a canine tooth. Concern about the possibility of infection of the pulp cavity of the maxillary canine teeth has been alleviated by awareness that normal marking behaviour often results in sufficient tooth wear to expose the pulp cavity (Figs. 5 and 6) [8].

5. Conclusions

Most adult male babirusa have normally orientated maxillary canine teeth. Approximately 12% of the animals in the wild experience erosion of the cranial bony tissues as a result of maxillary canine tooth growth. An additional group of babirusa (ca. 4%) escaped this problem due to the relative fragility of the dentine of their teeth and the tooth wear caused by their head-rubbing, scent-marking behaviour.

Disclosure of interest

The authors declare that they have no competing interest.

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