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An enigmatic hypoplastic defect of the maxillary lateral incisor in recent and fossil orangutans from Sumatra (Pongo abelii) and Borneo (Pongo pygmaeus).
--Manuscript Draft--

| Abstract: | Developmental dental pathologies provide insight into health of primates during ontogeny, and are particularly useful for elucidating the environment in which extant and extinct primates matured. Our aim is to evaluate whether prevalence of an unusual dental defect on the mesio-labial enamel of the upper lateral incisor, thought to reflect dental crowding during maturation, is lesser in female orangutans, with their smaller teeth, than males, and Sumatran orangutans, from more optimal developmental habitats, than those from Borneo. Our sample includes 49 Pongo pygmaeus (87 teeth), 21 P. abelii (38 teeth), Late Pleistocene paleo-orangutans from Sumatra and Vietnam (67 teeth), Late Miocene catarrhines Lufengpithecus lufengensis (2 teeth) and Anapithecus hernyaki (7 teeth). Methods include micro-CT scans, radiography and dental metrics of anterior teeth. We observed fenestration between incisor crypts and marked crowding of unerupted crowns, which could allow tooth-to-tooth contact. Tooth size does not differ significantly in animals with or without the defect, implicating undergrowth of the jaw as the proximate cause of dental crowding and defect presence. Male orangutans from both islands show more defects than females. The defect is significantly more common in Bornean orangutans (71%) compared to Sumatran (29%). Prevalence among fossil forms falls between these extremes, except that all five individual Anapithecus show one or both incisors with the defect. We conclude that maxillary lateral incisor defect is a common developmental pathology of apes that is minimized in optimal habitats and that such evidence can be used to infer habitat quality in extant and fossil apes. |

Dear Dr. Setchell:

Re: MS IJOP-D-16-00106

Thank you for your final suggested edits which I have made. I confirmed the author's name is Powe.

I will now proceed to final submission.

Regards

Mark

Response to Reviewer:
Firstly, I have made the changes requested by the Editor (just to be clear, no chimpanzees were examined for MLID in this study, only radiographed to get an idea of incisor crown formation in apes).

Secondly, I have simplified and enlarged Figure 3 (which relates to the topic just mentioned) and which the reviewer found difficult to read (as are all radiographs which are being replaced instrumentally by CT scans (our Figure 4)).

As recommended I have added into the Results section a small component to the micro-morphological observations; viz., *The purpose of Figure 6 is to show close-up morphological details of the outer enamel surface in: normal enamel; an area affected by MLID; as well as linear enamel hypoplasia.* **MLIDs show exposed Tomes' process pits in the floor of a plane form defect**. In addition, I have added, as recommended symbols to Figure 6 to try to make the observations in the dense prose from the Figure caption a bit more understandable.

Then, as recommended, I have added a larger section to the Discussion as follows:

Our micro-morphological analysis, which is limited to only the outer enamel surface of a cast (Fig. 6), found exposed Tomes' process pits in the floor of the defect. It can be concluded that there occurred an abrupt cessation of matrix secretion without recovery of function, at least centrally within the defect. At the time, the affected ameloblasts still possessed the distal portion of their Tomes' processes (Witzel, Kierdorf, Schulz, & Kierdorf, 2008). It can be inferred that, in terms of etiology, the proximate causative agent was a short-term event affecting a localized group of cells. This scenario is compatible with a sudden breaching of the inter-crypt septum creating a fenestration. Rather than invoking a gradual compression of a tooth crown within an unyielding crypt-a physical process that would have been detectable as a graduated secretory response from the ameloblast-it seems more likely, given the ledge-like appearance of many of the MLIDs (Fig. 5), that there was relatively abrupt abnormal contact of the developing crown with the sharp edge of a crypt fenestration. Histological thin sections of original teeth with MLID will be required to resolve these speculations.

Lastly, regarding Island differences and the reviewers concern about over-stressing habitat quality as an explanation, I have added the following caveat:

Rather than arguing for differences in habitat quality, it may be germane that lactation, which presumably provides a reasonably assured component of the infant's food requirements, is prolonged significantly longer in Sumatran than Bornean orangutans (van Noordwijk et al., 2013).

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Authors: Mark F. Skinner[1]
Matthew M. Skinner[2,3]
Varsha C. Pilbrow[4]
Darcy L. Hannibal[5,6]

1. Correspondence should be addressed to: mskinner@sfu.ca, +44 07583 412295, Department of Archaeology, King's Manor, University of York, York, YO1 7EP, United Kingdom

2. School of Anthropology and Conservation
    University of Kent
    Marlowe Building
    Canterbury, UK, CT2 7NR

3. Department of Human Evolution
    Max Planck Institute for Evolutionary Anthropology
    Leipzig, Germany, 04103

4. Department of Anatomy and Neuroscience
    University of Melbourne
    Parkville, VIC, 3010, Australia

5. Department of Population Health and Reproduction
    University of California, Davis
    One Shields Ave
    Davis, CA 95616

6. Brain, Mind and Behavior Unit
    California National Primate Research Center
    University of California, Davis
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8
9
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11   Department of Archaeology, King's Manor, University of York, York, YO1 7EP, United
12   Kingdom
13
14 2. School of Anthropology and Conservation
15   University of Kent
16   Marlowe Building
17   Canterbury, UK, CT2 7NR
18
19 3. Department of Human Evolution
20   Max Planck Institute for Evolutionary Anthropology
21   Leipzig, Germany, 04103
22
23 4. Department of Anatomy and Neuroscience
24   University of Melbourne
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26
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28   University of California, Davis
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30   Davis, CA 95616
31
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38   **Abstract**

39   Developmental dental pathologies provide insight into health of primates during ontogeny,

40   and are particularly useful for elucidating the environment in which extant and extinct

41   primates matured. Our aim is to evaluate whether prevalence of an unusual dental defect

42   on the mesio-labial enamel of the upper lateral incisor, thought to reflect dental crowding

43   during maturation, is lesser in female orangutans, with their smaller teeth, than males; and

44   Sumatran orangutans, from more optimal developmental habitats, than those from Borneo.

45   Our sample includes 49 *Pongo pygmaeus* (87 teeth), 21 *P. abelii* (38 teeth), Late Pleistocene

46   paleo-orangutans from Sumatra and Vietnam (67 teeth), Late Miocene catarrhines

47   *Lufengpithecus lufengensis* (2 teeth) and *Anapithecus hernyaki* (7 teeth). Methods include

48   micro-CT scans, radiography and dental metrics of anterior teeth. We observed

49   fenestration between incisor crypts and marked crowding of unerupted crowns, which

50   could allow tooth-to-tooth contact. Tooth size does not differ significantly in animals with

51   or without the defect, implicating undergrowth of the jaw as the proximate cause of dental

52   crowding and defect presence. Male orangutans from both islands show more defects than

53   females. The defect is significantly more common in Bornean orangutans (71%) compared

54   to Sumatran (29%). Prevalence among fossil forms falls between these extremes, except

55   that all five individual *Anapithecus* show one or both incisors with the defect. We conclude

56   that maxillary lateral incisor defect is a common developmental pathology of apes that is

57   minimized in optimal habitats and that such evidence can be used to infer habitat quality in

58   extant and fossil apes.

59

60   **Key words:** infancy; dentition; growth; paleohealth; *Lufengpithecus; Anapithecus*

2

Introduction

61

62   Primate growth is a reflection of metabolic function as influenced by nutritional and

63   disease factors within particular habitats (Altmann 1998). As large, slow-growing

64   mammals, whose tooth formation may span several years of nutritional and disease

65   seasonal cycles, the dental maturation of apes in the wild is sensitive to developmental

66   conditions (Zihlman *et al.* 2007). Teeth form within bone. Where cranio-facial bone growth

67   has been insufficient, erupted teeth in the adult mammal may be crowded and mal-

68   occluded (DiOrio *et al.* 1973; Luke *et al.* 1979; Thomaz *et al.* 2010; Tonge and McCance

69   1973). A mild relationship in humans was found between growth deficit (height for age)

70   and malnutrition and crowding of permanent teeth (2010). Severely undernourished pigs

71   show third molar impaction due to undergrowth of jaws in length (McCance and Ford

72   1961) and severe dental crowding with direct contact between adjacent teeth (Tonge and

73   McCance 1973). Calorie deficiency has a greater negative impact on jaw growth than does

74   protein deficiency (Luke *et al.* 1979). Experimental protein under-nutrition in rats induces

75   catabolism of muscle (including chewing muscles), reduced jaw size and dental crowding

76   (Garat *et al.* 2007). Non-human primates are no exception. A low protein diet in squirrel

77   monkeys delayed growth and shape changes, particularly in the masticatory region

78   (Dressino and Pucciarelli 1997).

79

80   Prior to eruption, dental crowns are normally sequestered in their own crypts during

81   formation; consequently there is almost no consideration of *pre-eruptive* dental crowding.

82   Indeed it has been remarked that "future studies of primate tooth development should

83   include data on times of crypt initiation and rates of crypt enlargement, without which

84   analyses of dental development are incomplete" (Boughner and Dean 2004) (P. 274).

85   Although these authors emphasize genetic control of taxonomic variation in normal

86   available space for successive crown mineralization, they also note that physiological or

87   physicochemical factors may establish baseline minimum distance maintained between

88   teeth from their inception. On occasion, alveolar bone (the inter-dental septum) that

89   normally separates crypts, may not be maintained, such that inter-crypt fenestration

90   occurs. Good evidence for crypt fenestration, labially or buccally, has been shown in the

91   case of localized hypoplasia of the primary canine (LHPC) in humans and apes (Skinner

92   1986, 2000; Skinner and Hung 1989; Skinner and Newell 2003) and a comparable defect of

93   the maxillary molars of pigs (Skinner *et al.* 2014). In terms of ultimate causation of crypt

94   fenestration defects, evidence suggests that vitamin A deficiency or reduced bioavailability

95   explains instances of LHPC in humans and other apes (Skinner *et al.* 1994; Skinner and

96   Newell 2003); and the combined effects of sickness and malnutrition in pigs (Skinner *et al.*

97   2014).

98

99   Ephemeral fenestration between adjacent crypts can allow contact in primary human teeth

100   (Lukacs 1999). For example, Lukacs describes areas of missing enamel on mesial and distal

101   surfaces of primary canines and on the mesial surface of molar teeth in archaeological

102   samples, terming these interproximal contact hypoplasias (IPCH). He suggests that in such

103   cases (about 15%) there was abnormally slow longitudinal growth of the jaws in infancy.

104   Enamel defects in IPCH range from single or confluent circular pits (ca. 0.5mm in diameter)

105   to "basins" several mm in length and breadth. Usually they are plane-form defects

106 "characterized by a broad area of deficient enamel...near the area of maximal mesial or

107 distal curvature of the crown" (Lukacs 1999) (P. 723). He writes:

108   The proximate etiology of IPCH is tooth-tooth contact through fenestrae in the inter-
109   dental septum due to anterior/posterior compaction of the developing dentition.
110   Developmental disruptions in bone growth due to nutritional or pathological insult,
111   combined with underuse and consequent reduction of the jaws, are possible factors
112   involved in the etiology of IPCH (ibid, p. 732).
113

114 Thus, it is reasonable to expect that compromised nutrition in infant apes will affect jaw

115 growth and possibly produce dental crowding, crypt fenestration, and contact hypoplasias.

116

117 Orangutans (*Pongo* species) were at one time broadly distributed from Southern China to

118 Java. Despite their clear success throughout a huge latitudinal range, orangutans are

119 described as having strict habitat requirements (i.e., evergreen wet forest) (Nater *et al.*

120 2011). During glacial periods of the Pleistocene, the climate in Sumatra was cooler, drier

121 and more seasonal (Harrison *et al.* 2006; Meijaard 2003). A review of the ecological

122 correlates of fossil orangutan find spots indicates that orangutans likely retreated to forest

123 refugia during the Pleistocene dessication which affected parts of the Sundaic region

124 (Ibrahim *et al.* 2013). Late Pleistocene environments of Sumatra are reconstructed on

125 ecological grounds to have been warm and wet, similar to today (Louys and Meijaard

126 2010). West Sumatra remained forested (Meijaard 2003). Nevertheless, land temperatures

127 during cold phases of the Pleistocene may have decreased by as much as 3-5°C (Harrison *et*

128 *al.* 2006).

129

130 At the end of the last ice age, a rapid rise in sea level isolated orangutans on the islands of

131 Borneo and Sumatra (Harrison *et al.* 2006), creating contrasting habitats to which they

132   have been adapting for some 14,000 years (Hanebuth *et al.* 2000). Bornean mammals, in

133   general, tend to be smaller than conspecifics in other locations, attributable to lower

134   primary productivity on relatively less fertile soils on Borneo (Meiri *et al.* 2008; Wich *et al.*

135   2011). There are several lines of evidence which suggest that Sumatra may currently

136   provide a superior habitat for orangutans due, fundamentally, to volcanically-derived soils

137   (Wich *et al.* 2011). Sumatran forests show higher soft-pulp fruit production, generally, and

138   throughout the seasons (Delgado and van Schaik 2000). Unlike Bornean orangutans (*Pongo*

139   *pygmaeus*), Sumatran orangutans (*Pongo abelii*) spend more time eating high-quality foods

140   such as fruit and insects and less time eating bark and vegetation (Russon *et al.* 2009).

141   Moreover, Sumatran orangutans seem less reliant on fallback foods than are Bornean

142   orangutans, being able to find figs and fruit year round (Russon *et al.* 2009). In Borneo,

143   there are months when fruit is a minor part of the diet whereas, in Sumatra, fruit is always

144   a major part of the diet (Morrogh-Bernard *et al.* 2009). Not surprisingly, orangutan

145   population density is higher in Sumatra than in Borneo (van Schaik *et al.* 2009). However,

146   our assessment of the Sumatran habitat for orangutans may be skewed by the high

147   densities of animals inhabiting the Kluet, Singkil and Tripa swamps in the northern corner

148   of the island whose peat soils are regularly inundated by rivers and run-off from adjacent

149   hills that bring minerals from the Leuser mountains, creating an optimum habitat for

150   growth and development that is judged to be exceedingly rare in Borneo (Husson *et al.*

151   2009).

152

153   In this study, we investigate an unusual dental defect that may be a marker of under-

154   developed cranio-facial growth in great apes. Maxillary lateral incisor defects (MLIDs) are

155   abnormalities of the mesio-labial enamel contour on the upper lateral incisor (Hannibal

156   2003) visible as pit, plane-form and/or notch defects, varying from a tiny dimple to a major

157   cleft occasionally affecting crown/root orientation (Fig. 1). MLIDs have been tentatively

158   attributed to a combination of systemic stress and local anatomical factors leading to pre-

159   eruptive, developmental crowding; to date, their presence is restricted to apes, especially

160   orangutans among whom they were reported to occur in about one-third of animals

161   (Hannibal 2003). Intriguingly, there are no human examples of MLID, although the more

162   severe examples of the defect reported below may have a parallel in the so-called J-shaped,

163   Etruscan Upper Lateral Incisor; however, the latter condition is located more mesio-

164   lingually (Pinto-Cisternas *et al.* 1995).

165

166

167   Our aims are to: 1) elucidate the proximate cause of MLID; and 2) determine whether

168   orangutan samples from different spatio-temporal contexts exhibit different frequencies of

169   MLIDs. To accomplish the first aim we examine radiographic and microtomographic scans

170   of developing dentitions of chimpanzees (*Pan troglodytes troglodytes*) and orangutans,

171   respectively. We then characterize variation in anatomical location and type of defect in a

172   range of catarrhine primates and test for correlations between MLID frequency and

173   anterior tooth size and sex since mild to marked sex differences in anterior tooth size,

174   especially for the canine, could potentially affect the degree of anterior tooth crowding and

175   the likelihood of MLID occurring. To accomplish the second aim we compare MLID

176   frequency between extant orangutans from Borneo and Sumatra and between each extant

177   sample and samples of Vietnamese and Sumatran paleo-orangutans. We predict that, were

178 the growth of an infant ape to falter, the physical relationships of the upper anterior teeth

179 will predispose them to MLID; specifically that the formation of the crown of the upper

180 lateral incisor should overlap that of the forming upper central crown, but will be later in

181 time and physically behind it; and that inter-crypt fenestration can occur. Moreover, MLID

182 should take the form of pits and plane-form depressions in the outer enamel surface and

183 resemble those described for inter-proximal contact hypoplasias in primary teeth (Lukacs

184 1999).

185

186 Fossil assemblages are likely to be composed of those individuals who died before their

187 time; i.e., they form a biased subset selected out of the living assemblage-a mortality cohort

188 (Wood *et al.* 1992). We predict that MLID will be more common in mortality cohorts

189 reflective of attritional deaths (most fossil assemblages) rather than catastrophic mortality

190 (hunted assemblages) (DeWitte and Stojanowski 2015; Wood *et al.* 1992). Additionally, we

191 predict that MLID will be more frequent among Bornean orangutans with relatively

192 impoverished soils (Meiri *et al.* 2008) than among Sumatran orangutans from more

193 optimal habitats (Husson *et al.* 2009). Furthermore, MLID will be more common in

194 Sumatran paleo-orangutans than extant orangutans, due to amelioration of habitats in the

195 Holocene (Meijaard 2003).

196

197

198 **Methods**

199 Given the comparative and epidemiological nature of this study including, potentially,

200 innate, ontogenetic and nutritional factors, we cannot determine the etiology of MLID with

201   certainty. This would require a specimen with demonstrably compromised development in

202   which an unerupted central incisor is creating a divot in a lateral incisor. To evaluate the

203   inference that a defect of formation on the mesio-labial surface of the permanent upper

204   lateral incisor (MLID) may be attributable to physical contact between forming incisor

205   crowns while still in their crypts, we compared radiographs of two immature chimpanzees,

206   from the region between Batouri and Lomie, Cameroon whose crania are curated in the

207   Powell-Cotton Museum, Quex Park, U.K.. We also imaged an immature recent orangutan

208   maxilla, probably Sumatran in origin (Thomas Koppe pers. comm.), borrowed from the

209   Institut für Anatomie und Zellbiologie Universitätsmedizin Greifswald, using a BIR ACTIS

210   225/300 high-resolution micro-CT scanner (130 kV, 100 μA, 0.25 brass filter, 1250

211   projections, 2 frame averaging, resultant isometric voxel size was 30 μm) housed at the

212   Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology

213   (Leipzig, Germany). We segmented the tooth crypts and associated alveolar bone manually

214   in Avizo 6.3® (Visualization Sciences Group, SAS) and created surface models of tissues

215   using the surface generation module.

216

217   **Study sample**

218   Our sample included 70 recent orangutans (Table 1). Most of these were taken from the

219   wild in the early 1900s with locations documented by collectors (Table 1). All recent

220   Sumatran animals in this study derive from the northern province of Aceh (especially the

221   Medan area (Drawhorn 1994)) while the Bornean animals sample all three subspecies of *P.*

222   *pygmaeus* (Wich *et al.* 2008) (Fig. 2).

223

224

225   We examined 76 fossil hominoid incisors for MLID (Table 2). We selected fossils either

226   because they are thought to be related to modern orangutans, or because the collection

227   contains a comparatively large number of upper lateral incisors. Our sample includes five

228   individual *Anapithecus hernyaki* represented by seven upper lateral incisors (Kordos and

229   Begun 2001; Nargolwalla *et al.* 2005) from the site of Rudabanya, Hungary, which is Late

230   Miocene (MN 9, 11.2 – 9.7 Ma) in age (Andrews and Cameron 2010; Begun *et al.* 2006).

231   *Anapithecus* is considered to be a small-bodied catarrhine, probably a pliopithecoid

232   (Kordos and Begun 2002). The site is located in a valley on what was once a peninsula, 1-2

233   km wide, projecting into the Central Paratethys sea (Kordos and Begun 2002). The

234   relatively large number of individuals and their immaturity suggest that the locality may

235   have provided an optimum habitat for the primate close to the core area of the home range

236   where most juveniles would be concentrated (Andrews and Cameron 2010).

237

238   We included two *Lufengpithecus*, which is thought to be a close relative of orangutans

239   (Harrison 2010). These fossils are from the site of Shi-Hui-Ba in Yunnan Province, China,

240   which consists of lignite deposits, judged to be Late Miocene (6.9－5.8 Ma) in age (Qi *et al.*

241   2006; Zhao *et al.* 2008), formed in beaver ponds into which the arboreal ape

242   *Lufengpithecus* fell (Badgley *et al.* 1988)*.

243

244   Fossil orangutans from Mainland Asia and Sumatra have larger teeth (ca. 15-20%) than

245   recent orangutans (Smith *et al.* 2011) which may predispose them to MLID. The paleo-

246   Sumatran orangutans in our sample are from several poorly dated cave sites in the Padang

247   Highlands, all of which can be considered Late Pleistocene (Table II, but see Harrison et al.

248   (2006)). The sample is made up, overwhelmingly, of teeth thought to derive from

249   porcupine nests which census a mortality cohort rather than a catastrophic-type

250   assemblage (Drawhorn 1994). There are 56 teeth from a minimum of 38 individuals. There

251   are currently no orangutans in southern Sumatra from where the fossil orangutans used in

252   this study are drawn. The Padang Highlands are south of the putative ecological Mt. Toba

253   volcano barrier (Wilting *et al.* 2012), suggesting that the paleo-Sumatran orangutans may

254   be genetically closer to extant Bornean than to north Sumatran orangutans.

255

256   The fossil orangutans from Vietnam in our study come from five cave sites ranging in age

257   from Late Middle to Late Pleistocene (Table II). The paleo-environment of the Late

258   Pleistocene orangutan sites of Hang Hum in Vietnam may have been more open/mixed

259   than observed at lower latitudes (Louys and Meijaard 2010). There are 11 teeth from a

260   minimum of 10 individuals.

261
262

263   **Imaging and measurement**

264   We made observations on original teeth for simple presence/absence of a defect in the

265   labial enamel contour (we ignored evidence of linear enamel hypoplasia) and then made

266   casts of more salient examples in araldite for examination at higher magnifications and for

267   illustrative purposes. Acknowledging that customary dental metrics on fully-formed

268   anterior tooth crowns may not have much relevance for transitory size during ontogeny of

269   tightly packed, differentially-formed, incomplete crowns prior to eruption, we,

270   nevertheless, collected traditional measures of incisor crowns (Hillson 1996) with Moore-

271   Wright electronic calipers (+/- 0.01 mm) on European collections, and on teeth from

272   American museums using sliding calipers, calibrated to the nearest 0.01 mm. We measured

273   mesio-distal length at the incisal edge, labio-lingual breadth at midpoint of the cervical-

274   incisal axis, and labial height from incisal edge to cervical margin on the labial aspect

275   (Pilbrow 2006). Our observations of MLID were incidental to other studies. Consequently,

276   we did not collect metrics on affected and unaffected teeth, except for those taken on paleo-

277   orangutans. Nevertheless, we could combine separate studies that fortuitously include the

278   same specimens.

279

280   We conducted macro-photography with a Keyence digital microscope VHX-100 and used a

281   Fisher Portable 200 x-ray machine (preset at 65 peak kilovoltage) to radiograph the

282   immature chimpanzee maxillae. We measured depth of defects on casts with a μsurf mobile

283   scanner, manufactured by NanoFocus AG, Oberhausen. We took measurements from a

284   single profile which traversed the deepest point of the defect parallel to the longitudinal

285   axis of the crown (so-called N-S axis), even though some defects are angled (Fig. 1, 5). We

286   took scanning electron micrographs of a cast with MLID in the imaging facility at the

287   University of York with a JEOL JSM-6490LV instrument.

288

289   **Statistical analysis**

290   In that observation of a defect was often not purposive, but incidental to other studies, the

291   prevalence statistics reported below are probably conservative. Because fossil assemblages

292   are typically comprised of isolated teeth that cannot be reliably assigned to individual

293   animals, it is rarely possible to match right and left teeth from an individual or to identify

294   sex. Hence, statistical analysis is performed in terms of only lefts, and only rights, compared

295   to the same in recent orangutans. We used Chi Square and Fisher's Exact Test (when any

296   cell frequency is <6) to examine differences in prevalence of the defect between islands and

297   sexes; and Student's 't' test for the effect of tooth size, performed with SPSS 22 (IBM 2013).

298   We set alpha at 0.05.

299

300   **Results**

301   **Aim 1: the proximate cause of MLID**

302   Radiographs of the upper jaw of infant chimpanzees (Fig. 3) show that central incisor

303   crown mineralization is advanced slightly over the lateral incisor but that the crypt for the

304   lateral incisor is situated further occlusally in some specimens (e.g., M475). Micro-CT scans

305   of an orangutan infant upper jaw show that, prior to eruption, the lateral incisor is located

306   behind the central and that fenestration can occur between incisor crypts (Fig. 4).

307

308

309   These variable anatomic relationships show that the precise points of contact between

310   incisor crowns vary. Defect locations, shape and size are also variable (Fig. 5). Most are

311   found on the mesio-labial contour of the lateral incisor crown in the cervical half and

312   occasionally encroaching onto the root. Size varies from a small dimple on the cingulum,

313   through a 1 to 2 mm length notch angling mesio-incisally, to a large wedge-shaped defect

314   with distorted alignment of crown and root. The full range of defect severity goes beyond

315   enamel hypoplasia to include effects on dentin formation. They resemble the pits and

316   plane-form depressions described for inter-proximal contact hypoplasias in human

317   primary teeth (Lukacs 1999) (Fig 5 A and E) but also include the very distinctive diagonal

318   ledges first noted by Hannibal (2003) (Fig 5 B and C); as well as gross distortion of crown

319   and root alignment (Fig 5 D).

320

321

322   Scanning electron microscopy of a large defect (Fig. 6) shows close-up morphological

323   details of three varieties of outer enamel surface: normal enamel (Fig 6H), an area affected

324   by MLID (Fig 6D), and linear enamel hypoplasia (Fig 6A).

325

326

327   **Effects of sex and tooth size**

328   MLID is significantly more common in males than females for Borneo, but not for Sumatra,

329   at both the tooth and the individual level (Table III).

330
331

332   We found no significant size differences between teeth from individuals with or without

333   MLID (Table IV). However, in 11 out of 13 comparisons, individuals with MLID had, on

334   average, bigger teeth (higher z-scores) than those without.

335
336
337

338   We found no significant differences between teeth with or without MLID in any dental

339   measure for both the paleo-Sumatran and Bornean orangutan samples (Table V).

340
341

342   Overall, MLID in recent animals occurs in 57% of upper lateral incisors and 59% of

343   individuals taken from the wild. Bilateral symmetry of the presence of MLID is the norm

344   (91%). There are no side differences in the occurrence of MLID in the combined orangutan

345   sample (Chi Square =0.111, df=1, P=0.740), nor in Bornean or Sumatran orangutans

346   considered separately (Chi Square=0.843, df=1, P=0.358; Chi Square=0.038, df=1, P=0.846,

347   respectively) (Table VI).

348

349   **Aim 2: Do orangutan samples from different spatio-temporal contexts exhibit**

350   **different frequencies of MLIDs?**

351

352   **Cohort source**

353   The prevalence of MLID is significantly higher in the paleo-Sumatran orangutans than in

354   recent Sumatran orangutans (Table VI, Left side - Pearson Chi Square=6.222, P=0.013;

355   Fisher's Exact Test P=0.028; Right side - Pearson Chi Square=8.125, P=0.004; Fisher's Exact

356   Test P=0.009), but does not differ significantly from recent Bornean orangutans (Left side -

357   Pearson Chi Square=0.004, P=0.952; Fisher's Exact Test P=1.000; Right side - Pearson Chi

358   Square=0.756, P=0.384; Fisher's Exact Test P=0.440).

359

360   Sample sizes for other fossil forms are too small for statistical analysis. The prediction, that

361   MLID would be more common in fossil forms than in recent ones, is not supported. Recent

362   Bornean orangutans are more affected than any fossil taxon (except *Anapithecus hernyaki*

363   from Hungary where all seven teeth from five individuals are affected).

364

365   **Island source**

366   There is a major difference in the occurrence of MLID between islands with Bornean

367   orangutans being significantly more affected than Sumatra (Table VII). Recent Sumatran

368   orangutans show much less MLID than do the fossil orangutans from the same island.

369   Indeed, extremes of prevalence are found between the two recent samples from Borneo

370   and Sumatra.

371

372

373   **Discussion**

374   In terms of proximate causation, MLID is more likely due to dental crowding in infancy,

375   rather than genetics, based on the following observations: a) the common occurrence of

376   MLID within and among ape taxa; b) its physical appearance corresponding to the form of

377   the central incisor with which it is so closely located; c) its clear difference in shape from

378   linear enamel hypoplasia; d) prior work which links compromised somatic/skeletal

379   development to crypt fenestration enamel defects (Lukacs 1999; Skinner *et al.* 2014); and,

380   finally, e) the dissimilarity of MLID to examples of genetic defects such as amelogenesis

381   imperfecta (Hart *et al.* 2003; Lygidakis and Lindenbaum 1987). We found that: a) MLID is

382   more common in males; b) tooth size has only a mild, statistically non-significant effect on

383   MLID; c) MLID is significantly more common in Bornean orangutans and least common in

384   those from Sumatra, with most fossil assemblages showing intermediate prevalence

385   between these two extremes.

386

387   In our explanatory model, inter-crypt fenestration is a necessary but not sufficient

388   explanation for MLID. While we have shown that inter-crypt fenestration occurs, we do not

389   know how common this phenomenon is. Inter-crypt fenestrae have been described

390   between crowded, unerupted I^2, C and P^3 in a juvenile gorilla from the Osmond Hill

391   Collection (Royal College of Surgeons) (Beynon *et al.* 1991). Nothing is known of the

392   developmental health or conditions of this animal.

393

394   Our micro-morphological analysis, which is limited to the outer enamel surface, shows

395   exposed Tomes' process pits in the floor of the defect. We conclude that matrix secretion

396   ceased abruptly without recovery of function, at least centrally within the defect. At the

397   time, the affected ameloblasts still possessed the distal portion of their Tomes' processes

398   (Witzel *et al.* 2008). We infer that, in terms of etiology, the proximate causative agent was a

399   short-term event affecting a localized group of cells. This scenario is compatible with a

400   sudden breaching of the inter-crypt septum creating a fenestration. Rather than invoking a

401   gradual compression of a tooth crown within an unyielding crypt - a physical process that

402   would have been detectable as a graduated secretory response from the ameloblast - it

403   seems more likely, given the ledge-like appearance of many of the MLIDs, that there was

404   relatively abrupt abnormal contact of the developing crown with the sharp edge of a crypt

405   fenestration. Histological thin sections of original teeth with MLID will be required to

406   resolve these speculations.

407

408   It is surprising that MLID, which we consider a crowding defect, is little if at all affected by

409   tooth size. There is a non-significant tendency for teeth with the defect to be slightly bigger

410   in most comparisons (Table IV); larger samples in future studies may confirm this trend.

411   Another crypt fenestration defect (LHPC) is more severe in bigger primary teeth from

412   infant apes (Skinner and Newell 2003). On current evidence, the preponderance of MLID in

413   male orangutans is not due to sexual dimorphism in tooth size. Rather, we think that MLID

414   is due to undergrowth of the upper jaw in the presence of anterior teeth whose sizes are

415   more tightly genetically controlled and less susceptible to epigenetic perturbation than is

416   bone formation in the maxilla and premaxilla (Lukacs 1999).

417

418   We found that fossil orangutans from Sumatra show significantly more MLIDs than do

419   recent Sumatran orangutans and that they show the same proportion of MLID as do

420   Bornean orangutans. There are two possible explanations for this observation. Anatomical

421   factors predisposing to MLID, due to shared genetic heritage between southern Sumatran

422   and Bornean orangutans (Nater *et al.* 2011), may over-ride island differences in habitat

423   quality. Alternatively, the quality of the habitat, in terms of developmental stress leading to

424   anterior tooth crowding, does not differ between Late Pleistocene Sumatra and recent

425   Borneo. We are not in a position to speculate on what might have changed in the habitat

426   between the Pleistocene and recent times in Sumatra beyond noting that the documented

427   demographic decline of Sumatran orangutans must, all else being equal, reduce

428   competition for nutritional resources among conspecifics. The high occurrence of MLID in

429   Late Pleistocene paleo-orangutans from southern Sumatra points to a need for further

430   research to separate the effects of mortality selection in fossil assemblages from a harsher

431   Pleistocene environment, both of which factors can be expected to increase the occurrence

432   of MLID.

433

434   We observed the highest prevalence of MLID in *Anapithecus* from Rudabanya, Hungary

435   among whom all five individual *Anapithecus* show one or both incisors with the defect. This

436   is the highest prevalence noted so far in any taxon and raises the possibility of marked

437   developmental stress related to nutrition and/or disease in some members of this taxon.

438   Such a conclusion is not incompatible with the inference that Rudabanya is a prime habitat

439   for *Anapithecus* (Andrews and Cameron 2010) since this is a mortality cohort possibly

440   created by predation of more vulnerable individuals in a primate troop (Kordos and Begun

441   2002). The presence of MLID in a pliopithecoid raises the strong likelihood that this

442   inferred form of dental crowding will be present in some Old World monkeys as well.

443

444   Recent evidence, based on the periodicity of repetitive linear enamel hypoplasia, suggests

445   that Bornean orangutans show a preponderance of semi-annual stress episodes, in contrast

446   to Sumatran orangutans, who showed mostly annual cycles (Skinner 2014). This difference

447   was interpreted as providing mild support for the notion of better habitat quality in

448   Sumatra (Skinner 2014). This contrasts with an earlier effort to compare postnatal

449   developmental stress in orangutans, which found no difference between the islands in the

450   prevalence of localized hypoplasia of the primary canine (LHPC), thought to be a marker of

451   bone thinning in infancy (Skinner and Newell 2003). However, LHPC occurs in the first few

452   months after birth while formation of the upper lateral permanent incisor crown spans

453   about age two to six years (Beynon *et al.* 1991). Hence, a crowding defect of enamel

454   formation (i.e., MLID) that occurs during the developmental life stage from full reliance on

455   breast milk to growing independent foraging by the infant orangutan (van Noordwijk *et al.*

456   2013) could be a useful marker of comparative developmental stress between island taxa

457   and more suitable than LHPC to examine ideas about differences in habitat quality.

458

459   MLID is much more common in males, and in recent orangutans from Borneo. These two

460   observations may be linked. In terms of craniofacial dimensions, male Bornean infant

461   orangutans may be up to 20% larger than females (Hens 2005). Extrapolating this

462   observation to nutritional need suggests that lactation demands from a male infant

463   orangutan are greater (but see van Noordwijk et al (2013)). Human mothers of male

464   infants can produce milk that has 25% greater energy content (Powe *et al.* 2010). Such an

465   adaptation, to respond to greater nutritional demand from male infants, might indicate that

466   male infant orangutans are more prone to developmental dental crowding under

467   conditions of relative food stress (as seems to pertain in Borneo (Knott 1998)).

468   Alternatively, rather than invoking a sex difference in metabolic requirements, there may

469   be sex differences in the ontogenetic acquisition of skilled foraging behaviors (Russon

470   2006). Also, rather than arguing for differences in just habitat quality between the islands,

471   it may be germane that lactation, which presumably provides a reasonably assured

472   component of the infant's food requirements, is significantly longer in Sumatran than

473   Bornean orangutans (van Noordwijk *et al.* 2013).

474

475

476   **Conclusion**

477   We examined the form and prevalence of an unusual defect of dental formation, observable

478   on the mesio-labial surface of the maxillary lateral incisor (MLID) of apes, that we think has

479   the potential to be a marker of compromised infant development and, by inference, habitat

480   quality. Our micro-CT scans and radiography combined with scanning electron microscopy

481   of enamel surfaces show inter-crypt fenestration, predisposing the unerupted lateral

482   incisor to direct 'tooth-to-tooth' or 'tooth-to-fenestrated crypt edge' contact with the

483   creation of abnormal enamel surfaces including pits, plane-form and ledge defects. Neither

484   lateral incisor crown size specifically, nor size of the anterior dentition generally, including

485   sexually dimorphic canine teeth, links to MLID. We conclude that undergrowth of the jaws,

486   not tooth size, is the major predisposing cause of the defect. There is more of a difference in

487   MLID occurrence between islands than between sexes. MLID is significantly more common

488   in Bornean orangutan individuals than in Sumatra, with males more affected than females.

489   We conclude that the better nutritional environment for growing apes in Sumatra

490   promotes more optimal jaw growth protecting them from MLID. Surprisingly, paleo-

491   orangutans from southern Sumatra are significantly more affected by MLID than are recent

492   (northern) Sumatran orangutans, not differing in this respect from Bornean orangutans.

493   Finally, given the generally high prevalence of this dental crowding defect in Bornean and

494   fossil orangutans spread from Vietnam to Sumatra, we conclude that the optimal

495   developmental environment for recent orangutans, currently prevailing in northern

496   Sumatra, is not typical of the broad spatio-temporal habitats of orangutans in the past.

497   Thus, while MLID can be proposed as a proxy for habitat quality among apes, its overall

498   utility may be limited to the detection of optimal habitats only.

499

500   **Acknowledgments**

21

511

512   **References**

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686
687

Figure Legends

Fig. 1. Labial view of right maxillary lateral incisor (cast) with defect (MLID). This example shows a commonly observed form with a diagonal notch (indicated by black line), encroaching onto the root (Tooth 107-44b, paleo-Sumatran orangutan 11484-L2, Lida Ajer Cave).

Fig. 2. Source of museum specimens of orangutans where provenience within islands is known.

Fig. 3. Radiographs of the maxillary incisor region of two, younger and older, infant chimpanzees: A. female M475, m2 root apex open; B. male M173, m2 root apex closed. Note visual superimposition of the less mineralized/formed lateral incisor crown and incisal edge and crypt wall of the more mineralized/formed central incisor crown.

Fig. 4. 3D reconstruction from micro-CT scan of unerupted incisors in orangutan infant UGAZ 14.5.8 with completed milk dentition showing the relationship of the permanent maxillary incisors during crown formation and fenestrated inter-crypt septa (top right panel). Note superimposition of the incisal edge of the central incisor on the mid-crown region of the lateral incisor crown (bottom left panel).

Fig. 5. Variation in size and shape of the developmental dental defect in maxillary lateral incisors (casts) in a variety of primates. Specimens are turned so the defect is orthogonal to the viewer. Most north-south measures (in mm) are single profiles taken through the

712   deepest part of a defect (in microns) (except where noted). The rectangular area

713   demarcated in 'A' is reproduced in Figure 6. A. 107-42b: paleo-Sumatran orangutan 11485-

714   L48, Lida Ajer Cave, left**;** B. 107-43b: paleo-Sumatran orangutan 11484-L11, Lida Ajer Cave,

715   right**;** C. 107-44b: paleo-Sumatran orangutan 11484-L2, Lida Ajer Cave, right**;** D. 107-45b:

716   paleo-Sumatran orangutan 11488-44, left, mean profile across defect width is shown**;** E.

717   165b: siamang 11670-1, left**;** F. 130: Rud 97 *Anapithecus hernyaki* A.7, Loc.II 1989, left**;** G.

718   314: *Lufengpithecus lufengensis* YV622, left.

719

720   **Fig. 6**: Scanning electron microscope images of a cast in araldite of a paleo-orangutan left

721   upper lateral incisor 11485-L48, Lida Ajer Cave, Sumatra. **A.** Example of enamel hypoplasia

722   pit that is <u>not</u> a maxillary lateral incisor defect (MLID); note little worn Tomes' process pits

723   (★) within the sequestered surface of defect on left side of panel, indicating premature,

724   abnormal cessation of secretion by enamel-forming cells. **B.** Close up of deepest part of an

725   MLID showing the floor of the defect on the left and shoulder of defect on the right. Faint

726   ridges on the shoulder on the right side of panel represent normal enamel increments

727   called perikymata (dashed arrows). MLID contours of floor and shoulder do not conform to

728   normal enamel internal structure. **C.** Floor of MLID showing abnormal exposure of

729   somewhat worn Tomes' process pits (★) (enamel surface exposed to normal wear). **D.** Low

730   power overview of MLID; root to left side of panel, cervical part of enamel crown on right

731   side of panel. This example is large. Bubble artifacts in the deepest part of the defect can

732   also be seen in panel B. **E.** Junction of floor of defect with slope of the shoulder (on right).

733   On the left side, the floor of the defect is obscured by foreign matter that has been partially

734   cleaned out (see groove on upper right). **F.** Junction of root (left) surface with enamel

735   (right); both are normal in appearance. **G.** Floor of defect with faintly visible, worn Tomes'

736   process pits on upper left obscured, on lower and right sides, by a layer of foreign matter.

737   **H.** Normal, worn labial enamel.

738

MLID Tables with Headings-26Aug16

Table I. Sample of extant orangutans examined for MLID

Island	Male	Female	Sex unknown	Total
Borneo	16	30	3	49
Sumatra	13	7	1	21
Total	29	37	4	70

Table II. Sample of fossil hominoid lateral incisors examined for MLID

Taxon	N	Minimum number of individuals	Source	Date
Anapithecus hernyaki	7	5	A	MN9, 11.2 – 9.7 Ma [1]
Lufengpithecus lufengensis	2	2	B	Late Miocene, 7 Ma[2]
Paleo-orangutan Vietnam total	11	10	C	
Dieu Cave	1			undated Pleistocene
Hang Hum	1			140-80K[3], end Pleistocene[4]
Hoa Binh	1			undated Pleistocene[5]
Lang Trang	7			150K[6], Mid-Pleistocene[7],80-60K[8]
Tham Om	1			250-140K[3], Late Pleistocene[4]
Paleo-orangutan Sumatra total	56	38	D	
Djamboe	5			56-85K[9], 60-70K[11], Early Hol[12]
Sibrambang	22			Pleist./Holo.[9], 128-118K[10,13], 80K[13]
Lida Ajer	19			>80K[9, 11], IS. 5e[7,13], Early Hol[12]
Unspecified	10			
Total	76			

Source: A. Geological Museum Budapest; B. Zoological Institute, Kunming; C. Institute of Archaeology, Hanoi; D. Naturalis, Leiden

Dating references: 1. Begun et al. 2006 (MNI also based on this article); 2. Ho 1985; 3. Bacon et al. 2006; 4. Harrison 2000; 5. Bacon and Long 2001; 6. Jon de Vos (pers. comm.); 7. (Long *et al.* 1996); 8. Bacon et al. 2004; 9. Drawhorn 1994-Lida Ajer dates from [18]O Stage 4 >71K; 10. de Vos 1983; 11. van den Bergh et al. 1996; 12. Harrison et al. 2006; 13. Louys 2011

Table III. Sex differences in MLID expression in recent orangutan samples

Sample	Sex	Comparison	N	Yes/No	% Yes	Chi Square[1]	P
Borneo	Male	Teeth	29	27/2	93.1		
	Female	Teeth	53	32/21	60.4	9.947	0.002
	Male	Individuals	16	15/1	93.8		
	Female	Individuals	30	18/12	60.0	5.863	0.015
Sumatra	Male	Teeth	23	8/15	34.8		
	Female	Teeth	14	2/12	14.3	1.854	0.173
	Male	Individuals	13	5/8	38.5		
	Female	Individuals	7	1/6	14.3	1.266	0.260

1. Fisher's Exact Tests were run on all comparisons above (as some groups had less than five cases) and yielded identical patterns of significance.

Table IV. Comparison of tooth size[1] from extant orangutans with and without MLID.

Tooth	Measure	With MLID		Without MLID		Student's		Mann-Whitney	
		N	Mean	N	Mean	't'	P	Value	P
Central incisor	Mesio-distal	6	0.0874	17	-.0309	0.262	0.796	-0.140	0.889
	Labio-lingual	6	0.0970	16	-0.0364	0.294	0.772	-0.295	0.768
	Crown height	5	0.4624	13	-0.1778	1.375	0.188	-1.626	0.104
	Volume	5	0.4288	13	-1.2534	1.956	0.068	-1.922	0.055
Lateral incisor	Mesio-distal	8	-0.0938	18	0.0417	-0.334	0.741	-0.444	0.657
	Labio-lingual	8	0.1477	18	0.0656	0.434	0.674	-0.444	0.657
	Crown height	8	0.1412	18	-0.0628	0.504	0.619	-0.722	0.470
	Volume	8	0.1537	18	-0.0683	0.549	0.588	-0.167	0.868
Canine	Mesio-distal	7	-0.0941	16	0.0411	-0.314	0.756	-0.735	0.462
	Labio-lingual	7	0.455	16	-0.1993	1.610	0.122	-1.604	0.109
	Crown height	7	0.0416	15	-0.0194	0.141	0.890	-0.035	0.972
	Volume	7	0.1836	15	-0.0857	0.626	0.538	-0.458	0.647
All	Volume	5	0.3398	10	-0.1699	1.054	0.311	-0.980	0.327

1. Size is expressed as z-scores (i.e., deviation of a measure from the 'sex plus island' mean for that measure)

Table V. Dental measures (mm) of upper lateral incisors with and without MLID in Paleo-sumatran, Sumatran and Bornean orangutans
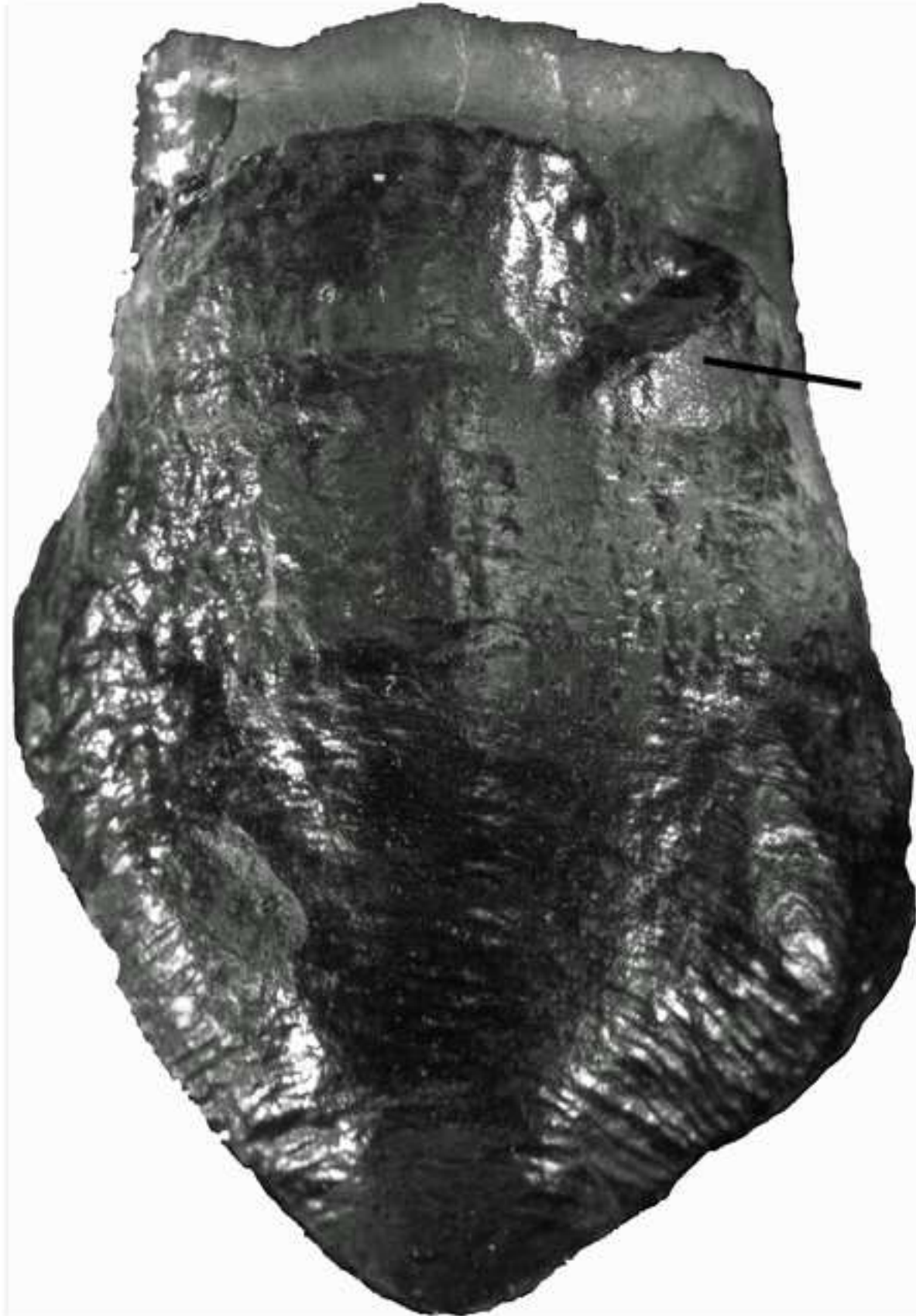
Measure	N	With MLID Mean	SD	N	Without MLID Mean	SD	Student's 't'	P
Paleo-sumatran								
Mesio-distal	30	8.99	1.01	11	8.96	0.76	0.097	0.923
Labio-lingual	27	9.34	1.10	11	9.20	1.03	0.366	0.717
Crown height	7	12.71	1.52	8	12.38	1.19	0.484	0.637
Volume	5	1109.07	326.20	3	1271.02	233.24	-0.743	0.486
Sumatran								
Mesio-distal	0	-	-	10	8.27	0.96	N/A	
Labio-lingual	0	-	-	10	7.87	0.54	N/A	
Crown height	0	-	-	10	10.30	1.54	N/A	
Volume				10	683.17	191.01	N/A	
Bornean								
Mesio-distal	8	8.58	0.62	8	8.40	0.78	0.518	0.613
Labio-lingual	8	8.66	0.80	8	8.31	0.44	1.118	0.283
Crown height	8	11.78	1.42	8	11.07	1.67	0.928	0.369
Volume	8	890.44	227.11	8	775.02	162.44	1.169	0.262

Table VI. Frequency of MLID in fossil and recent hominoid upper lateral incisors

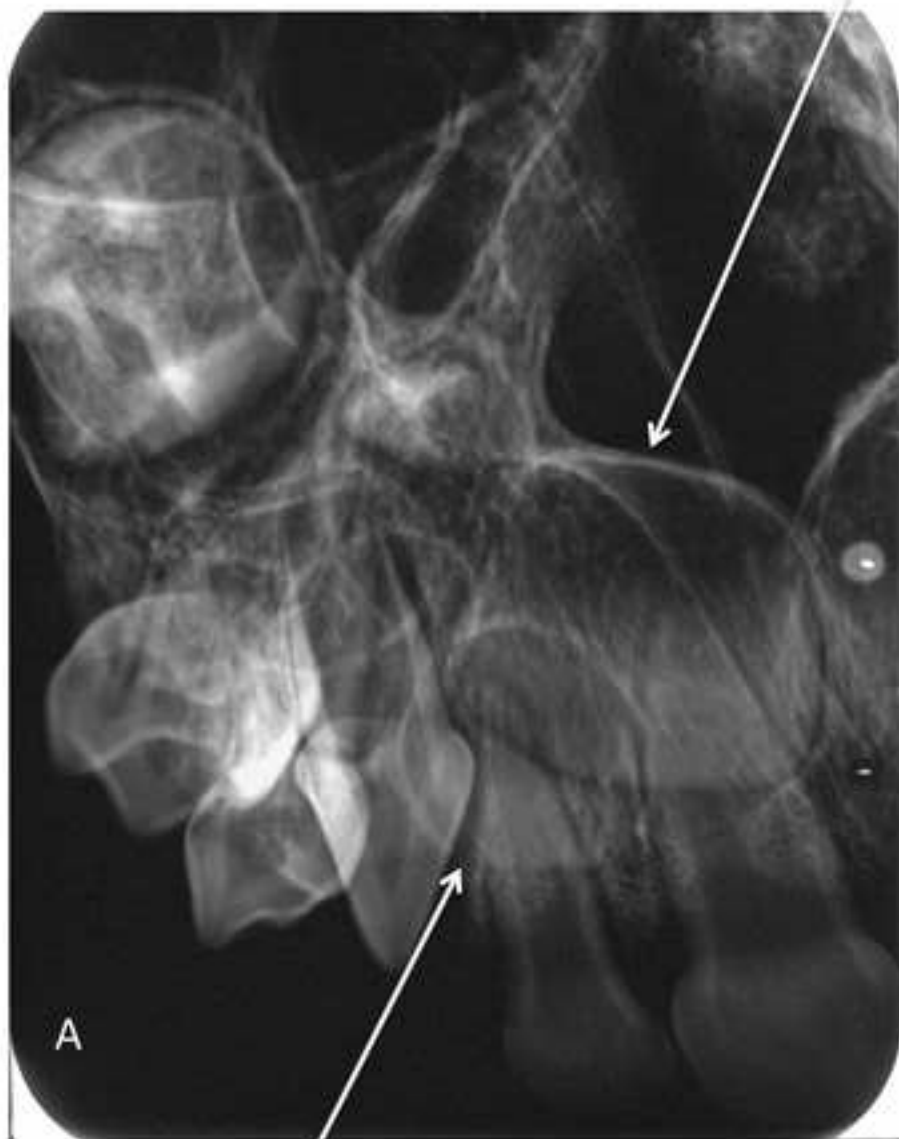| Sample	Side	N	Yes/No	Affected (%)
L. lufengensis	Left	2	1/1	50.0
	Right	-		-
	Combined	2	1/1	50.0
A. hernyaki	Left	4	4/0	100
	Right	3	3/0	100
	Combined	7	7/0	100
Paleo-orangutan				
Sumatra	Left	24	16/8	66.0
	Right	32	21/11	65.6
	Combined	56	37/19	66.1
Vietnam	Left	8	3/5	37.5
	Right	3	3/0	100
	Combined	11	6/5	54.5
All paleo	Left	32	19/13	59.4
	Right	35	24/11	68.6
	Combined	67	43/24	64.2
Recent Borneo	Left	47	31/16	66.0
	Right	40	30/10	75.0
	Combined	87	61/26	70.1
Recent Sumatra	Left	18	5/13	27.8
	Right	20	5/15	25.0
	Combined	38	10/28	26.3
All recent	Left	65	36/29	55.3
	Right	60	35/25	58.3
	Combined	125	71/54	56.8

Table VII. Distribution of MLID between recent orangutans from Borneo and Sumatra

Comparison	Sample	N	Yes/No	% Yes	Chi Square	P
Teeth	Borneo	87	61/26	70.1		
	Sumatra	38	10/28	26.3	20.68	<0.001
Individual	Borneo	49	35/14	71.4		
	Sumatra	21	6/15	28.6	11.13	<0.001

Figure 1

Figure 2

Total from Borneo=49

Aru Bay (12)

Adji (1)

Medan

Deli

Ketambe

Kinabatangan

Roema Manuel (1)
Mt. Kenepai

Sekayam River (6)

Menganne River
(1)

Tarutung

?Sama (2) and
Semandong (4) Rivers

Sintang

0°

Pontianak

Sekalau

Samarinda

Sempang River (7)

Gunung Palung

Batu Jurong (1)

Boentok

Barito river (2)

Toba

Kendawangan (4)
and Mambuluh (1)
Rivers

Tanjun Puting

Padang
Highlands

Total from Sumatra=21

Figure 3

Click here to download Figure Fig. 3.tif ⬇

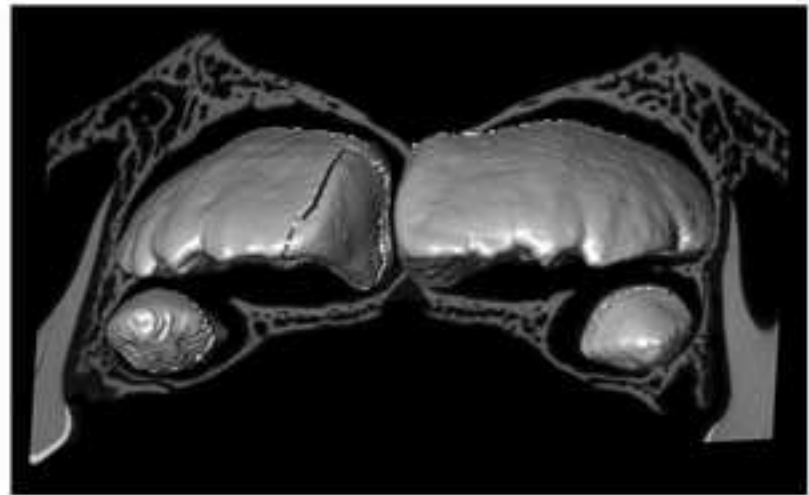Central incisor crypt and forming crown

Lateral incisor crypt and less formed crown
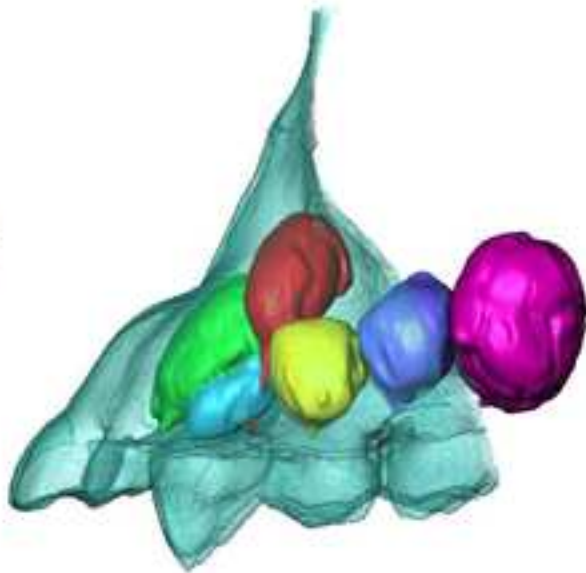
Figure 4

Occlusal of maxilla
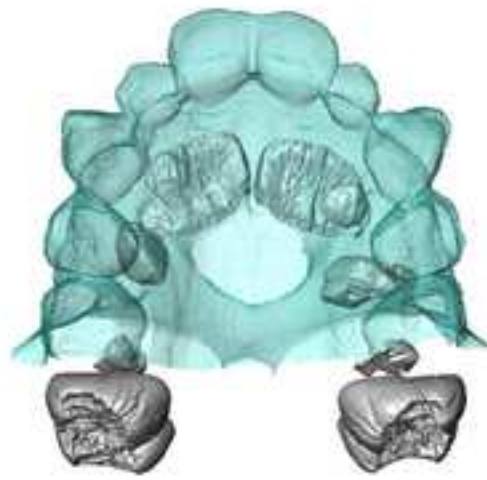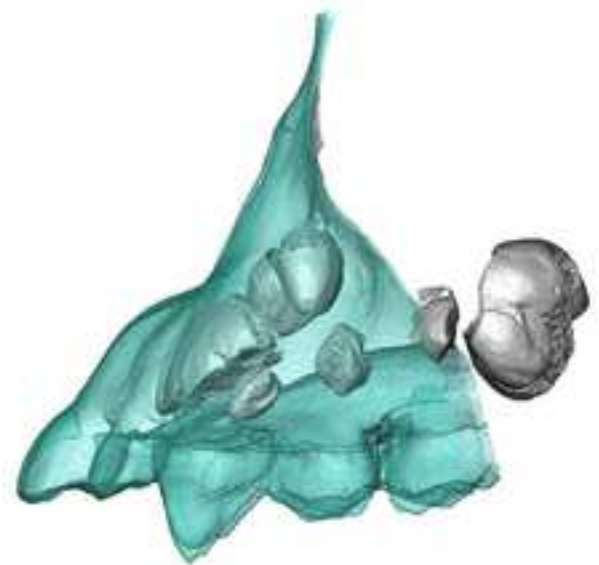
Occlusal of germs

Incisal edges with crypt fenestration

Tooth germs mesial view

Crypts on left side

Germs on left side

Figure 5

A

N-S height=3.43mm
Depth=752µm

B

N-S height=1.19mm
197µm

C

N-S height=1.84mm
226µm

D

N-S height=3.09mm
872µm

E

N-S height=1.00mm,
Depth=156µm

F

N-S height= 0.868mm
73µm

G

defect length= 3.74mm
267µm

Figure 6