

1 **Exploration of the taxonomy of some Pleistocene Cervini (Mammalia,**  
2 **Artiodactyla, Cervidae) from Java and Sumatra (Indonesia): a geometric- and**  
3 **linear morphometric approach**

4  
5 Ben Gruwier<sup>a,b\*</sup>, John de Vos<sup>c</sup> and Kris Kovarovic<sup>a</sup>

6  
7 a Department of Anthropology, Durham University, South Road, Durham, United Kingdom

8 b Department of Experimental Anatomy, Vrije Universiteit Brussel, Laarbeeklaan 103, Jette, Belgium

9 c Naturalis Biodiversity Center, Raamsteeg 2, Leiden, The Netherlands

10

11 **Abstract:**

12 *Third molars of extant- and fossil Southeast Asian deer were metrically compared using a linear- and geometric morphometric approach*  
13 *and discussed in relation to known taxonomic information from the literature. Our analysis suggests the presence of medium sized deer of*  
14 *the genus *Axis* and large sized taxa of the genus *Cervus* s. l. in Java. *Axis lydekkeri* and *A. javanicus* are considered valid taxa, with *A.*  
15 *lydekkeri* probably related to the subgenus *Hyelaphus*. The large deer, such as *Cervus kendungensis*, *C. stehlini* and *C. problematicus* are*  
16 *most likely of the subgenus *Rusa*, the former two closely related to extant *C. timorensis*. The Sumatran fossils are members of the subgenus*  
17 **Rusa*, but not necessarily conspecific with extant *Cervus (Rusa) unicolor*.*

18 **Keywords:** Cervidae, Cervini, taxonomy, Quaternary, Sundaic subregion, geometric morphometrics

19 *\*Corresponding Author: Department of Anthropology, South Road, Durham University, Durham, United Kingdom, , email: B.J.Gruwier@durham.ac.uk*

20 **1. Introduction**

21

22 Due to the presence of a sizable number of hominin remains (Kaifu *et al.* 2005) and the diverse fauna  
23 that has been found in association with them, the Pleistocene paleontological deposits of Java are  
24 recognized as some of the richest in Southeast Asia (e.g. Dubois 1907, 1908, Von Koenigswald 1933,  
25 1935). Systematic collection of fossils since the late 19<sup>th</sup> century eventually led to the description of  
26 the *Pithecanthropus erectus* - (now *Homo erectus*) lectotype and resulted in the description of large  
27 numbers of mammalian remains from Java and Sumatra (de Vos 2004).

28 After more than a century the description and taxonomic status of most large mammal groups from  
29 this region has been discussed in detail (e.g. von Koenigswald 1933, 1935, Hooijer 1948, 1955, 1958,  
30 1960, 1962, Hardjasmita 1987 ). However, this is not the case for Cervidae since the family is  
31 morphologically conservative in nature (Lister 1996), complicating the identification and inferred  
32 taxonomic status of the often fragmentary remains. Consequently more than a dozen taxa have been  
33 described for the Pleistocene of Java over the course of the last century (e.g. Martin 1888, Dubois  
34 1907, Stremme 1911, von Koenigswald 1933, 1934). The validity of some of these species can be  
35 questioned.

36

37 Geographically this paper is concerned with the Pleistocene deer of Sundaland, which is the name  
38 given to the biogeographical region that includes Borneo, Sumatra, Java, Bali, Palawan, the Mentawai  
39 Islands and the Malay Peninsula up to the Kra Isthmus (Harrison *et al.* 2006). In the past it also  
40 included the landmass in between these islands that emerged during periods of lower sea level (Voris  
41 2000). In practice the emphasis of this work is on Sumatra and especially on Java, as pre-modern  
42 mammal fossils are scarce in the other regions of Sundaland.

43

44 While the taxonomy and phylogeny of extant deer remains partially unresolved, recent genetic and  
45 morphological studies have shed new light on this complex family (Groves & Grubb 1987, Randi *et al.*  
46 1998, Pitra *et al.* 2004, Meijaard & Groves 2004,). Here we synthesize several decades of research to  
47 provide an overview of the medium- and large sized fossil cervids described from the Pleistocene  
48 deposits of Java and Sumatra. We further explore through morphometric analysis how some of these  
49 palaeospecies may be related to extant taxa in the light of recent taxonomic insights. Although the  
50 results of our analysis may provide some additional data on extant deer relationships, it is not our  
51 intention to give a complete taxonomic revision of the recent Cervidae.

52 The focus of this paper is on the true antlered deer or the tribe Cervini. Muntjaks (*Muntiacus* spp.)  
53 also form part of the Pleistocene faunas of Java and Sumatra (Badoux 1959, Van den Brink 1982, de

54 Vos 1983), but don't pose the same problems in terms of (applied) taxonomy and are not included in  
55 this study.

56

57 Cervini are known from large parts of Eurasia, North Africa and America (Meijaard & Groves 2004),  
58 but tropical Asia was probably the heartland of deer radiation (Geist 1998). Since the Neogene and  
59 especially during the Quaternary much of this radiation was induced by increasing climatic  
60 fluctuations. This led to significant changes in Cervid ecology, behavior and morphology over time  
61 (Geist 1998).

62 In Southeast Asia, an area of major importance in deer evolution, regional geography and  
63 environments are thought to have been heavily influenced by Pleistocene glacio-eustatic sea level  
64 fluctuations (Van den Bergh *et al.* 2001). At times of lower sea level, large parts of the Sunda shelf  
65 must have been exposed, connecting major islands like Borneo, Sumatra and Java to the Asian  
66 mainland (Bird *et al.* 2005, Voris 2000) (fig.1). Undoubtedly these changes must have had an effect  
67 on speciation in certain mammal groups (Cranbrook 2010).

68 <Fig. 1>

69 A number of Cervini are currently present in Eurasia (fig. 2). As with most of the other deer tribes,  
70 the taxonomy of the Cervini remains controversial (Groves 2007). An overview of the taxonomic  
71 scheme followed in this paper is given below.

72 <Fig. 2>

73 In the classic work by Groves and Grubb (1987), the genus *Cervus* (sensu lato) is divided into four  
74 subgenera, namely *Rusa* (containing *C. timorensis*, *C. unicolor*, *C. alfredi* and *C. mariannus*), *Rucervus*  
75 (containing *C. eldii*, *C. duvaucelli* and *C. schomburgki*), *Prezwalskium* (containing only *C. albirostris*)  
76 and *Cervus* (sensu stricto) (containing *C. elaphus* and *C. nippon*). The genus *Axis* is composed of the  
77 subgenera *Axis* (containing *Axis axis*) and *Hyelaphus* (containing *Axis kuhlii*, *Axis calamianensis* and

78 *Axis porcinus*) (Meijaard & Groves 2004). The Genus *Dama* is represented by only one species (*Dama*  
79 *dama*), while Pere David's deer (*Elaphurus davidianus*) may have been the result of hybridization  
80 between two unknown species (Groves & Grubb 1987), most likely from the *Rucervus* and *Cervus*  
81 subgenera (Meijaard & Groves 2004).

82 More recent genetic research has shed doubt on some of these relationships. Using mitochondrial  
83 DNA sequences Randi *et al.* (2001) argued for a fusion of the subgenera *Rucervus* and *Elaphurus*,  
84 while also proposing a revision of the subgenus *Rusa*. Another mitochondrial DNA analysis by Pitra *et*  
85 *al.* (2004) proposes several changes on the generic level as well as at the species level. In that study  
86 (Pitra *et al.* 2004) genera are demarcated using a 5 mya time criterion, resulting in the recognition of  
87 the genera *Rucervus* (with *R.duvaucelli* and *R. schombrugki*), *Axis* (only containing *Axis axis* and  
88 excluding *Hyelaphus*) and *Dama* (with *Dama dama* and *Dama mesopotamica* separated as true  
89 species). All other species were placed in *Cervus*, with possibly *Cervus eldii* under its own genus  
90 *Panolia* and *Cervus davidianus* under its own genus *Elaphurus* (Pitra *et al.* 2004). In addition *Cervus*  
91 *elaphus* was argued to be paraphyletic and *Axis porcinus* more closely related to the *Rusa*-deer than  
92 to *Axis axis* (Pitra *et al.* 2004).

93 As these analyses remain sometimes incompatible (see overview table 1), we chose to maintain a  
94 relatively conservative view regarding living deer taxonomy based on the scheme by Groves and  
95 Grubb (1987), but keeping in mind more recent developments. A summary of the taxonomic scheme  
96 used in this paper is given in table 1.

97 <Table 1>

## 98 **2. The Pleistocene Cervini from Java and Sumatra**

99 Southeast Asian Pleistocene deer are known from the mainland (e.g. Auetrakulvit 2004, Zeitoun *et al.*  
100 2005, Bacon *et al.* 2008a, 2008b) as well as from several islands west of Wallace's line (Van den

101 Bergh *et al.* 2001). As far as Sundaland is concerned, deer fossils are found in deposits from Borneo,  
102 Sumatra, Java, Peninsular Malaysia and Palawan.

103 The paleontological record of Java is by far the best known in the region (Louys *et al.* 2007). Cervids  
104 have been identified in a number of sites. Two of the living Cervini are currently found in Java, *Cervus*  
105 (*Rusa*) *timorensis* and *Axis* (*Hyelaphus*) *kuhlii*. Both are known from the paleontological record in  
106 addition to a series of extinct taxa, a large number of which have been described by von Koenigswald  
107 (1933, 1934). A list of taxa known from the Javanese Pleistocene record and their synonyms is  
108 summarized in table 2. Of the extinct species only *Axis javanicus*, *Cervus zwaani*, *Axis lydekkeri* and  
109 *Cervus problematicus* are recognized by the International Commission on Zoological Nomenclature  
110 (ICZN) (Polaszek *et al.* 2005).

111 The Bawean deer (*Axis kuhlii*), that currently has a distribution limited to Bawean island north of  
112 Java, is thought to have been present on the main island of Java at least during the early Holocene, as  
113 supported by finds from Wajak cave (Van den Brink 1982). Its relationship with the Pleistocene deer  
114 from Java is not well understood.

115 <Table 2>

116 *Cervus* (*Rusa*) *timorensis* is almost certainly present in several Holocene cave deposits such as  
117 Sampung cave (Dammerman 1934), Wajak cave (van den Brink 1928) and Hoekgrot (Storm 1990).  
118 *Cervus hippelaphus* described at the Middle Pleistocene locality of Ngandong by von Koenigswald  
119 (1934) is a junior synonym for *Cervus* (*Rusa*) *timorensis* (Hedges *et al.* 2008) and *Cervus* sp., known  
120 from the Late Pleistocene Punung fauna (Badoux 1959, Westaway *et al.* 2007), might also belong to  
121 this species. Besides this, a large number of specimens from the various Pleistocene localities of Java  
122 have been attributed to the sub-genus *Rusa*, but it is unclear whether they should be included in  
123 *Cervus* (*Rusa*) *timorensis* (Zaim *et al.* 2003).

124 Another extant species mentioned for the Javanese Holocene record is *Cervus (Rucervus) eldii*  
125 (Dammerman 1934). A single incomplete antler from Sampung cave was identified by Dammerman  
126 (1934). The author describes the fragment as peculiar due to the fact that the brown tine forms an  
127 almost continuous curve with the beam. Similar specimens from the Middle Pleistocene site of  
128 Ngandong were however described by von Koenigswald (1933) as a subspecies of *Cervus* (now *Axis*)  
129 *javanicus*. No other fragments of *C. eldii* are known from Java.

130 A smaller species, *Axis lydekkeri*, was described by Martin (1888) on the basis of a single antler. The  
131 almost complete antler is smooth, groove-less (Martin 1888) and has a typical lyre-shape (Zaim *et al.*  
132 2003). The type specimen probably belongs to a sub-adult individual (Dubois 1908). This species is  
133 relatively well known and identified by several different researchers (Dubois 1908, Vogel von  
134 Falckenstein 1910, Stremme 1911, von Koenigswald 1933, 1934). Although Martin (1888) considered  
135 its morphology different from any known recent deer, it was Dubois (1891) who noticed its similarity  
136 to the Indian *Axis*-deer. Meijaard and Groves (2004) argue that it should probably be classified under  
137 the subgenus *Hyelaphus*. *Axis lydekkeri* is abundant in Trinil (von Koenigswald 1934), but also present  
138 at several other sites such as Pitu, Watualang (von Koenigswald 1933), Ngandong (von Koenigswald  
139 1934) and Sangiran (Moigne *et al.* 2004a, 2004b). It is thought to be similar in size to *Axis (Hyelaphus)*  
140 *porcinus* (Zaim *et al.* 2003) and slightly smaller than *Axis (Axis) axis* (Vogel von Falckenstein 1910).

141 *Axis javanicus*, another member of the genus *Axis*, was described by von Koenigswald (1933, 1934).  
142 No type specimen was designated, but many antler pieces are known from late Quaternary contexts  
143 in eastern Java (Zaim *et al.* 2003). This species is best known from Ngandong (von Koenigswald 1933)  
144 in addition to Watualang, Pandejan and possibly Pitu (Zaim *et al.* 2003). The antlers of this species  
145 are described as slightly pearled and, unlike *Axis lydekkeri*, with an angle between the beam and  
146 brown tine of at least 90° and usually with an accessory tine within this angle (von Koenigswald 1933,  
147 Zaim *et al.* 2003). According to Moigne (2004) it is most similar in size to *Axis (Hyelaphus) kuhlii*, and  
148 might be considered a subspecies of this taxon. Meijaard and Groves (2004) on the other hand

149 consider it synonymous with- or closely related to- a form of the extant chital (*Axis axis*), that  
150 migrated from the mainland to Java during the Late Pleistocene.

151 *Cervus zwaani* (von Koenigswald 1933) is based on four mandibles and an upper third molar from  
152 Bumiaju in Western Java. In addition, von Koenigswald provisionally attributed some fragments from  
153 Parning (von Koenigswald in de Terra & Patterson 1939, de Terra 1941), Sangiran and Baringinan  
154 (von Koenigswald 1934) to this species. No antlers have been attributed to *Cervus zwaani* (Zaim *et al.*  
155 2003), but von Koenigswald (1933) claimed the species was slightly larger than *Axis lydekkeri* and  
156 that the premolars were more robust than in the latter species. According to Zaim *et al.* (2003), this  
157 species may however be a junior synonym of *Axis lydekkeri*, because it is morphologically  
158 indistinguishable from this species and the supposed larger size is not supported by comparative  
159 measurements on *A. lydekkeri* fossils in the collections in Leiden (Zaim *et al.* 2003, Bouteaux 2005).

160 Besides these animals of smaller stature that might be attributed to the genus *Axis*, there are also a  
161 series of larger deer known from the Javanese paleontological record. The majority of these have  
162 been assigned to the subgenus *Rusa*. Their relationship with the only species of this subgenus living  
163 today in Java (*Cervus (Rusa) timorensis*), remains controversial.

164 One of these larger taxa is *Cervus stehlini*. This species was described on the basis of several  
165 mandibles and a few antler fragments from the Early Pleistocene Bumiaju locality (von Koenigswald  
166 1933). Von Koenigswald (1933) considered it distinct from *Cervus hippelaphus* (now *Cervus (Rusa)*  
167 *timorensis*), based on the peculiar morphology and slenderness of its premolars. Besides these small  
168 differences however, the author noted its similarity in size and shape to the living form (*C.*  
169 *timorensis/C. hippelaphus*) (von Koenigswald 1933).

170 The largest species recognized in the fossil record of Java is *Cervus (Rusa) problematicus*. This taxon  
171 was described by von Koenigswald (1933) from the Early Pleistocene of Bumiaju on the basis of a  
172 partial cranium and a lower first molar. Later von Koenigswald (1934) included other remains in this

173 species and placed it under the subgenus *Rusa*. The skull has recently been re-identified as a bovid  
174 and should be excluded from this taxon (van den Bergh pers. comm. in Zaim *et al.* 2003).

175 The taxonomic status of *Cervus (Rusa) oppenoorthi* is also debated. This species is known from a  
176 number of antler fragments from Pitu and Semboengan and was described as strongly pearly and  
177 similar to *Cervus kuhlii* (now *Axis (Hyelaphus) kuhlii*), but larger in size (von Koenigswald 1933). Von  
178 Koenigswald (1933) considered it distinct from the large Javanese *Rusa (Cervus (Rusa) timorensis)*  
179 and from *Axis lydekkeri*. He furthermore concluded that it was probably most closely related to *Axis*  
180 (*Hyelaphus) kuhlii*. This was later confirmed by van Bemmelen (1944), who considered it possibly even a  
181 subspecies of *A. kuhlii*. Zaim *et al.* (2003), on the other hand have argued that it was probably more  
182 closely related to the *Rusa*-subgenus. It should however be noted, that at the time von Koenigswald  
183 classified these specimens, the Bawean deer (now *Axis (Hyelaphus) kuhlii*), was considered a member  
184 of the subgenus *Rusa* (von Koenigswald 1933). Moreover the taxonomic position of *Hyelaphus* is still  
185 a matter of controversy and some recent molecular studies support a close relationship between this  
186 subgenus and the *Cervus (Rusa) timorensis/Cervus (Rusa) unicolor*-clade (Pitra *et al.* 2004).

187 Besides those already mentioned, von Koenigswald (1933) also noted the presence of several forms  
188 in the fossil record that he could not assign to a specific taxon. Whether these finds should be  
189 considered separate species from the ones mentioned here, is unclear. In Watualang he found a very  
190 small but badly preserved antler fragment that he was unable to assign to a species and therefore  
191 identified it as *Cervus* sp. Later in the same publication, the author mentions a partial skull with  
192 antlers from Sembungan that he does not identify (von Koenigswald 1933). The author noticed its  
193 similarity to both *Cervus (Rusa) unicolor* and to *Cervus (Rusa) timorensis*. However, due to the  
194 unusual morphology of the cranium, notably a sharp kink in the skull profile, it was not included in  
195 any of the known species, but cautiously placed under *Cervus (Rusa)* sp. (Von Koenigswald 1933).

196 Others also noticed the occurrence of other, larger species in the Javanese deposits. In 1888, Martin  
197 mentioned the presence of a larger sized deer (*Cervus* sp.), besides *Axis lydekkeri*, amongst the

198 known Javanese fossils at that time. Dubois (1891) came to the same conclusion, and also  
199 acknowledged the existence of at least two different deer amongst the fossils he had collected in the  
200 field. Although at the time he did not yet assign these finds (*Cervus* sp.) to a new species, he  
201 mentioned that the antlers were much heavier than the ones of *Axis lydekkeri* (Dubois 1891). He  
202 made a similar statement in 1907 adding that "...the other, rarer deer species are similar in shape to  
203 the large deer living in Java today [*Cervus timorensis*], but also to a certain extent to the Indian  
204 Sambar [*Cervus unicolor*]." (Dubois 1907). In the absence of a type specimen, it is unclear what fossil  
205 material the author was referring to in these cases. Furthermore other researchers have also  
206 provisionally attributed cervid fossils to the subgenus *Rusa* without identifying them to species.  
207 These include *Cervus* sp. sensu Stehlin (1925), *Cervus* sp. sensu Stehn & Umgrove (1926) and *Cervus*  
208 (*Rusa*) sp. sensu Aziz & de Vos (1999).

209 A new species of large stature that was described by Dubois is *Cervus kendengensis* (Dubois 1908).  
210 This form was considered similar to the recent *Cervus hippelaphus* (now *Cervus (Rusa) timorensis*). It  
211 was given specific status mainly due to the shorter and thicker antlers (Dubois 1908). Although  
212 Dubois (1908) gave only a short description and did not designate any type specimens, a sizable  
213 number of the larger Cervidae in the collection of the Naturalis were placed by him under this taxon.

214 In the same publication (Dubois 1908) the author also proposed a new species: *Cervus*  
215 *palaeomendjangan*. In his description, Dubois characterizes this second large Cervid by the peculiar  
216 morphology of its antlers with typically small tines pointing outwards and to the front, similar to the  
217 recent large Javanese deer (*Cervus (Rusa) timorensis*). This species was not recognized by von  
218 Koenigswald (1933).

219 Of special interest in other areas of Sundaland are a number of remains found in cave deposits in the  
220 Padang highlands of Sumatra. Based on their biostratigraphic similarity to the Javanese Punung  
221 fauna, these sites can probably be dated in the early Last Interglacial (between 128 +/-15 and 118 +/-

222 3 ka) (de Vos 1983, Westaway *et al.* 2007). Dozens of isolated teeth were found in these caves.  
223 Besides Muntjak (*Muntiacus muntjac*) a large deer of the (sub-) genus *Rusa* is present (de Vos 1983).  
224 A number of cave sites in Borneo (Harrison 1998, Piper *et al.* 2008) have provided evidence of  
225 cervids, but the Pleistocene record in Borneo does not go back further than about 45,000 years (Niah  
226 cave) and contains only extant species like sambar (*Cervus unicolor*) and muntjak (*Muntiacus* sp.)  
227 (Cranbrook 2010). The fossil record in peninsular Malaysia is particularly poor. A small collection  
228 from Ipoh (Kinta Valley, Perak), thought to be of Middle Pleistocene age, possibly contains a large  
229 deer of the (sub-) genus *Rusa* (Hooijer 1962). In some recently collected material of uncertain age  
230 (from Perak and Selangot) the presence of *Cervus unicolor* was attested (Ibrahim *et al.* 2012). Several  
231 late Pleistocene fossils from cave sites in peninsular Thailand (Thung Nong Nien, Moh Khiew I, II and  
232 Lang Rongrien) were also identified as *Cervus unicolor* (Auetrakulvit 2004).

233 Palawan island is considered part of the Sundaic biogeographic region as well (Reis & Garong 2001).  
234 The Pleistocene fossil record in Palawan goes back to the late Pleistocene in Tabon (Fox 1970) and Ile  
235 cave (Piper *et al.* 2011) and contains fossils of two deer species, namely *Axis (Hyelaphus)*  
236 *calamianensis* and a larger species identified as *Cervus (Rusa)* sp.

237 <Table 3>

### 238 **3. Materials and methods**

239 Identification criteria for some Pleistocene Cervini have been based on slight morphological and  
240 metric differences, supported by limited sample sizes. A more extensive morphometric analysis of  
241 deer fossils may confirm whether or not some of the proposed size differences between species are  
242 still valid when compared to a larger dataset. Qualitative or non metric definition of morphological  
243 characters is inherently subjective to a certain extent (Degusta & Vrba 2005) and since morphological  
244 differences between Southeast Asian deer species are particularly subtle, linear- and geometric  
245 morphometrics were deemed appropriate complementary techniques to assess whether observed

246 morphological differences can be quantified. Table 3 gives an overview of the analyzed fossil species  
247 with comments on their validity and hypothesized taxonomic status. All the analyzed fossil taxa come  
248 from Java and Sumatra.

249 More specifically, a comparative morphometric study of recent and fossil Cervini was performed on  
250 the upper- and lower third molars. We chose to focus on teeth, as these elements often retain their  
251 integrity after deposition (Albarella *et al.* 2009). This is even more so the case in Southeast Asian  
252 Pleistocene deposits, where osseous material is often reduced to dental remains due to rodent-  
253 (*Hystrix* sp.) gnawing (de Vos 1983, Bacon *et al.* 2008). Besides that, teeth are more helpful in  
254 taxonomic studies than postcranial elements as they are usually conservative in their structure  
255 (Degerbol 1963, Payne & Bull 1988) and furthermore they allow for large modern samples, because  
256 museum collections are often composed of skulls rather than complete skeletons.

257 The third molar was considered to be particularly useful because it suffers less from interproximal  
258 abrasion than the other molars (Cucchi *et al.* 2009). In addition, the *lower* third molar has the  
259 advantage that it is easily identifiable even if found in an isolated state. Therefore two approaches  
260 were taken: a linear morphometric approach on the lower m3 and a geometric morphometric  
261 analysis of the upper M3.

262

### 263 **3.1 Materials**

264 A total number of 283 fossil specimens were measured at Naturalis in Leiden and 33 specimens were  
265 photographed at the same institute for geometric morphometric analysis. Additionally, an extra 25  
266 fossil molars were measured at the Indonesian Center for Geological survey, Bandung. A few  
267 measurements were taken from the literature (Bouteaux 2005,), while those from the Pleistocene of  
268 Laos and Vietnam were provided by A.M. Bacon and her collaborators (Bacon *et al.* 2008a, 2008b and  
269 unpublished data).

270 As the absolute dating of many of these fossils as well as the sites they come from is controversial  
271 (e.g. Indriati *et al.* 2011) and beyond the scope of this paper, we only give a broad indication of the  
272 age when discussing individual sites. The material from Bumiaju, Trinil, Kedung Brubus, Sangiran,  
273 Ngebung and Ngandong is of Early – Middle Pleistocene age (de Vos *et al.* 1982, de Vos 1985, van  
274 den Bergh *et al.* 2001, Bouteaux 2005). Wajak (Storm *et al.* 2013), Punung, (de Vos *et al.* 1982, de Vos  
275 1985, Storm 1995, van den Bergh *et al.* 2001), the Sumatran Cave assemblages (de Vos 1983), Tam  
276 Hang (Bacon *et al.* 2008a) and Duoi U’oi (Bacon *et al.* 2008b) are of Late Pleistocene age.

277

278 Linear- (128 specimens) and geometric morphometric data (81 specimens) on recent deer were  
279 collected at the following institutes: the Natural History Museum of Rotterdam, the National  
280 Museums of Scotland, the British Museum of Natural History, the National Museum of Natural  
281 History Paris, the Royal Belgian Institute of Natural Sciences, the Zoological Museum University  
282 Ghent, the Swedish Museum of Natural History, the Morphology Museum University Ghent and the  
283 osteological reference collections of the universities of Durham and Lille. Sample sizes for some  
284 species are very low due to their extreme rareness in museum collections. Table 4 provides an  
285 overview of the number of specimens collected for each species.

286 Pathological specimens were systematically excluded and teeth with a severe degree of attrition,  
287 which complicated the placement of landmarks, were avoided in the geometric morphometric  
288 analysis. Right molars were photographed for gmm-analysis, but a number of left ones were virtually  
289 mirrored using TPSdig 2.16 and included in this study as well. Although captivity is known to affect  
290 morphology in certain mammals (O’Regan & Kitchener 2005), due to the scarcity of some species in  
291 museum collections, zoo specimens were also included to maximize sample size. A table with the  
292 original measurements taken by the authors has been provided in appendix A (fossil specimens) and  
293 appendix B (extant specimens).

294 <Table 4>

## 295 **3.2 Methods**

### 296 **3.2.1 Linear morphometrics**

297 As a first approach to address these issues, a linear morphometric analysis was applied on a set of  
298 fossil deer teeth in addition to a number of recent deer specimens. Measurements of maximum  
299 length and width were taken with calipers following Heintz (1970) and expressed in millimeters. The  
300 resulting data was plotted on a XY-graph using PAST 2.17b. Inter-rater reliability was tested on a  
301 small sample (N=14) of *A. lydekkeri* specimens. Measuring differences were visually assessed using a  
302 Bland-Altman plot (Bland and Altman 1986). Although relatively simple, ratios between linear  
303 measurements have been successfully applied on cervid fossils as a means to discriminate between  
304 taxa (e.g. Heintz 1970, Bouteaux 2005, Castanos *et al.* 2006, 2012, Liouville 2007, Lister *et al.* 2010).  
305 Statistical significance between groups was assessed using a Multivariate Analysis of Variance  
306 (MANOVA) in PAST 2.17b. As molar measurements are not thought to be substantially affected by  
307 sexual dimorphism in other ungulates (Payne & Bull 1988, Kusatman 1991), both male and female  
308 individuals were combined in the dataset to ensure a maximum sample size. The majority of the  
309 measurements are original, with the exception of the *Axis* sp.-specimens from Ngebung and the  
310 *Cervus unicolor* specimens from mainland Southeast Asia.

### 311 **3.2.2 Geometric morphometrics**

312 Alongside a traditional morphometric approach, a number of teeth were also analyzed using  
313 geometric morphometrics (GMM). Previous research on ungulate remains (e.g. Cucchi *et al.* 2009,  
314 2011., Evin *et al.* 2013a, 2013b, Brophy *et al.* 2014) has shown that digital image analysis of dental  
315 morphology can be used to study phenotypic diversity. The drawback of selecting the upper third  
316 molar for analysis is that, opposed to the lower third molar, it can be confused with the second- or  
317 even the first molar when found in an isolated state. Despite these complications, we chose the  
318 upper M3 because it was more prevalent in museum collections (crania are more common than  
319 mandibles) and because our preliminary studies on the lower molars provided less promising results.

320 This was possibly in part due to the lack of useful homologous traits that could be easily landmarked.  
321 Therefore a method was developed to quantitatively differentiate upper molars based on a ratio  
322 between their anterior and posterior width (fig. 3). This was based on the observation that the  
323 difference in width between the paracone and protocone (anterior width, AW) becomes increasingly  
324 larger relative to the difference in width between the metacone and hypocone (posterior width, PW),  
325 from the first to the third upper molar. Based on this ratio an attempt was made to identify  
326 individual molars. Using this method on fossil teeth, a number of third molars was selected that  
327 could be used for further analysis.

328 <Fig. 3>

329 The advantage of using geometric morphometrics is that size can be analyzed separately from shape  
330 (Viscosi & Cardini 2011). It also has the ability to analyze anatomical elements as whole units instead  
331 of a number of independent measurements (Zelditch et al. 2004, Curran 2009). As size has often  
332 been a criterion used to assign fossil cervids to specific taxa, an independent approach was also  
333 considered a useful way to test how well taxonomy is reflected by size differences.

334 Therefore the first part of this analysis was to test on a reasonably large sample if the upper M3 can  
335 be used to differentiate deer at species level and to assess whether morphological differences reflect  
336 a taxonomic signal. In the second phase a number of Pleistocene fossils were included and compared  
337 to the dataset of recent species.

338 Morphological variation in the molars was quantitatively analyzed using a geometric morphometric  
339 model where shape was defined by placing a series of homologous landmarks at discrete anatomical  
340 loci on the individual teeth (Zelditch *et al.* 2004). The resulting Cartesian coordinate data were, after  
341 the appropriate transformations, compared with PAST 2.17b.

342 Using a Nikon D90 camera, photographs were taken of the molars from the occlusal perspective.  
343 Teeth were fixed with plasticine on a supporting platform and leveled using a spirit level. The buccal

344 wall was systematically placed at a 90° angle with the supporting platform and the camera was  
345 positioned at 27 cm from the object while focusing on the junction between the enamel and the  
346 root.

347 A total number of 13 landmarks were placed along the outline of the protoconid and hypoconid using  
348 TPSdig 2.16 (Rohlf 2004) (fig. 4). Landmarks were only placed on those parts of the molar that were  
349 not subject to tooth wear to avoid measuring age-related shape differences. The analysis made use  
350 of a combination of type 1- and type 2- landmarks and a series of sliding semilandmarks. Type 1  
351 landmarks have the strongest homology and are defined as locations where multiple discrete tissues  
352 intersect at a single point (Baab 2012). Type 2 landmarks have no true biological correspondence, but  
353 an emulated homology is supported by the geometry of the surrounding anatomy (Baab 2012). In  
354 semilandmarks only the wider structure or surface where the landmarks are positioned is  
355 homologous (Baab 2012).

356 <Fig. 4>

357 Only landmark III can be defined as a type 1 landmark. Landmark II is defined as the most extreme  
358 point of the protoconid, while landmark I is placed at distance  $x$  from landmark II on the anterior  
359 portion of the outline, where  $x$  equals the linear distance between landmark II and III. Landmark IV is  
360 defined at the same distance ( $x$ ) from landmark III along the outline of the hypoconid. As these three  
361 landmarks only have a geometric correspondence, they can be described as type II landmarks. In  
362 addition three series of semilandmarks were placed in between these four type I/II landmarks.

363 Given the inherently arbitrary location of the semilandmarks, additional treatment was needed to  
364 improve the one to one correspondence of these points (Bookstein 1997). Using TPSrelw 1.49 (Rohlf  
365 2005) semilandmarks were slid along homologous curves between the above mentioned type 1 and  
366 type 2 landmarks (Bookstein 1997). The *minimize procrustes distance*-option was used as a sliding  
367 method. This procedure removes the difference along the curve in semilandmark positions between

368 the reference form and the individual specimens by estimating the direction tangential to the curve  
369 and removing the component of the difference that lies along this tangent (Sheets *et al.* 2004).

370 Besides that, TPSrelw was also used for a generalized procrustes superimposition of the complete set  
371 of landmarks. By overlaying homologous landmarks and minimizing procrustes distances (Goodall  
372 1991), objects were scaled, rotated and translated to exclude information that is irrelevant to  
373 differences in shape (Walker 2000). During the generalized procrustes superimposition shape  
374 coordinates are projected in a euclidian space tangent to the procrustes shape space (Viscosi &  
375 Cardini 2011). Whether this approximation in tangent space is good enough for further statistical  
376 analysis was tested with TPSSmall 1.20 (Rohlf 2003) on a procrustes datamatrix with all specimens  
377 included.

378 To assess the repeatability of the digitization protocol, six specimens were randomly photographed  
379 and landmarked five times using the same standardized protocol. This test was based on the protocol  
380 by Adriaens (2007) and was performed to evaluate whether the used methodology allows for any  
381 significant errors to occur during the digitization process of the landmarks (Cucchi *et al.* 2011). When  
382 performing a principle components analysis (PCA) on these five replicates, the same individuals are  
383 expected to cluster together.

384 PAST 2.17b (Hammer *et al.* 2001) was used for all statistical analyses of the resulting coordinate data.  
385 Several multivariate analyses were performed to explore morphological variation in cervid molar  
386 shape. Principle component analysis (PCA) was primarily used to explore how species clustered  
387 together in groups and to reduce the amount of variables for potential further analysis. All shape  
388 variables were included in order to identify the greatest axes of molar shape variation in the dataset  
389 (Cucchi *et al.* 2011). Shape changes along the axes of the different relevant components were  
390 visualized using thin plate spline deformation grids. A permutational multivariate analysis of variance  
391 (NPMANOVA) was run on the most relevant principle components to determine statistical  
392 significance between designated groups. Further, a Canonical Variates Analysis (CVA) was run on

393 certain selected groups to maximize the between groups variability, to test the significance of shape  
394 differences and to determine the relationships between different species.

395 Although the generalized procrustes analysis excludes all size differences, it does not eliminate the  
396 effects of allometry (Curran 2009). Therefore, the results of the relevant components were regressed  
397 against log centroid size to test whether there was a correlation between size and shape.

## 398 **4. Results**

### 399 **4.1 Linear morphometric analysis**

400 A visual inspection of a Bland-Altman plot of mean differences in measurement (not shown)  
401 suggested there was no consistent bias between observers. In fig. 5 linear measurements are plotted  
402 of the maximum length and width of fossil deer teeth from Java. Although subtle morphological  
403 differences are not taken into account here, several conclusions can be drawn from the data in  
404 relationship to what is known from the literature. The Pleistocene *Axis lydekkeri* (open squares) are  
405 clearly the smallest species known from the fossil record. Although there is slight overlap with the  
406 fossil *Cervus kendengensis* specimens (stars) from the collection in Leiden, both species separate  
407 reasonably well in different clusters and the results of a MANOVA (table 5) indicate a significant  
408 difference ( $p < 0.001$ ). The clusters suggest a disparity between at least a larger form and smaller form  
409 in the fossil record.

410 In a comparison in figure 7 of *Axis lydekkeri* (open squares) with the living members of the genus  
411 *Axis*, it appears to overlap with both *Axis (Hyelaphus) kuhlii* (dots) and *Axis (Hyelaphus) porcinus*  
412 (open diamonds), but is generally smaller than the Indian *Axis (Axis) axis* (crosses). The MANOVA  
413 (table 5) however indicated not only significant differences between *A. lydekkeri* and *A. axis*  
414 ( $p < 0.001$ ), but also between *A. lydekkeri* and *A. porcinus* ( $p = 0.010$ ). Differences between *A. lydekkeri*  
415 and *A. kuhlii* were not significant ( $p = 0.467$ ).

416 Comparing *Axis javanicus* (vertical rectangles) with the other paleospecies (fig. 5), it becomes clear  
417 that, although placed under the genus *Axis*, it does not cluster well with the smaller specimens in our  
418 dataset, and is more similar in size to the (presumed) *Rusa* deer like *Cervus kendengensis* ( $p=0.079$ ,  
419 stars). This is confirmed by comparison with measurements of recent Southeast Asian species (fig. 6).  
420 *A. javanicus* falls within the range of the living *Cervus (Rusa) timorensis* ( $p=0.687$ , filled squares).

421 When on the other hand, the measurements of *A. javanicus* are plotted against the measurements of  
422 extant deer from the genus *Axis* (Fig. 7), it becomes clear that *Axis javanicus* (vertical rectangles) is  
423 significantly larger than *Axis (Hyalaphus) porcinus* ( $p=0.002$ , open diamonds) and the fossil *Axis*  
424 *lydekkeri* ( $p<0.001$ , open squares), but falls well within the size range of the living Indian *Axis (Axis)*  
425 *axis* ( $p=0.100$ , crosses).

426 <Table 5>

427 <Fig. 5>

428 <Fig. 6>

429 <Fig. 7>

430 <Fig. 8>

431 *Cervus zwaani* (fig. 5, filled diamonds) appears to be part of the cluster of smaller species. From  
432 comparison with the other small paleospecies from Java and extant members of the genus *Axis* (fig.  
433 7), it appears to be similar in length to the other *Axis* deer, yet somewhat wider. The MANOVA (table  
434 5) suggests it is significantly different from *Axis lydekkeri* ( $p<0.001$ , open squares), recent *Axis (Axis)*  
435 *axis* ( $p<0.001$ , crosses) and *Axis (Hyalaphus) porcinus* ( $p=0.042$ , open diamonds), but not from the  
436 *Axis* sp. specimens from Ngebung. According to von Koenigswald (1933) its teeth are supposedly  
437 larger and more robust than those of *A. lydekkeri*. But Zaim *et al.* (2003) pointed out, this size  
438 difference is not confirmed by comparative measurements with *A. lydekkeri*. Although the third

439 molar may be slightly more robust, there is considerable visual overlap in size between the two  
440 forms. The *Axis* sp. specimens from the Pleistocene site of Ngebung (fig. 7, filled triangles) are not  
441 significantly different from *Axis lydekkeri* ( $p=0.365$ ). Although *Cervus oppenoorthi* (not in the graphs)  
442 cannot be ruled out as another candidate for *Axis* sp., it was impossible to include this species in the  
443 analysis due to the fact that it is only known from antler fragments.

444 When comparing the larger Javanese deer with living representatives of the subgenus *Rusa* (fig. 6), it  
445 becomes clear that there is size overlap between the several different groups. *Cervus kendengensis*  
446 (fig. 6, crosses) was considered by Dubois to be comparable in shape to extant *Cervus (Rusa)*  
447 *timorensis* (Dubois 1908). While the morphometric data (fig.6) does indeed suggest a similarity of this  
448 form to the subgenus *Rusa*, the visual overlap with recent *Cervus (Rusa) timorensis* (filled squares) as  
449 well as with the living *Cervus (Rusa) unicolor* (open squares) complicates interpretation. That size  
450 may not be a good indicator for taxonomic differences between *Rusa*-species, is also suggested by  
451 limited metric differences between fossil- (inversed filled triangles) and recent *Cervus (Rusa)*  
452 *timorensis* (filled squares).

453 The fossil *Cervus stehlini* (fig. 6, ellipses) was another species considered by von Koenigswald (1933)  
454 to be closely related to *Cervus (Rusa) timorensis* (filled squares), which is confirmed by our linear  
455 morphometric data. *C. stehlini* is not significantly different from extant *C. timorensis* ( $p=0.685$ ) and  
456 fossil *C. timorensis/hippelaphus* ( $p=0.080$ ), but is from *C. unicolor* ( $p<0.001$ ). Von Koenigswald (1933)  
457 recognized it as a separate species, mainly due to its particularly slender premolars. Even though the  
458 premolars of this species were not included in this analysis, it should be noted that the lower third  
459 molar is not particularly slender and can even be said to plot out between the rather robust teeth  
460 within the extant *Cervus (Rusa) timorensis*-group.

461 *Cervus (Rusa) problematicus* (fig. 6, cross) is clearly much larger than any of the known fossil- or  
462 recent Javanese deer. It falls within the spectrum of extant *Cervus (Rusa) unicolor* (open squares), but  
463 whether it should be considered synonymous is unclear.

464 In fig. 8 measurements of Pleistocene *Cervus (Rusa)* sp. from Sumatra (open triangles) have been  
465 plotted against recent members of the subgenus *Rusa* and fossil *Cervus (Rusa) unicolor* from Tam  
466 Hang, Laos (Bacon *et al.* 2008a, Bacon *et al.* unpublished data, dots), Duoi Uoi, Vietnam (Bacon *et al.*  
467 2008b; Bacon *et al.* unpublished data, filled triangles) and Lang Trang, Vietnam (Long *et al.* 1996,  
468 stars). Again the data indicate that caution is advised when using size to differentiate between *Rusa*-  
469 deer. The measurements from Duoi Uoi suggest a wider size range in fossil *Cervus (Rusa) unicolor*  
470 than what would have been expected from the recent *C. unicolor* sample (open squares). This is  
471 evidently based on the assumption that the fossils from Duoi Uoi should indeed all be placed under  
472 this species. Nevertheless the *Cervus (Rusa)* sp. sample from Sumatra (open triangles) is clearly larger  
473 than the living *Cervus (Rusa) timorensis* ( $p < 0.001$ , filled squares) and the Phillipine *Rusa* species,  
474 *Cervus (Rusa) alfredi* ( $p < 0.001$ , circles) and *Cervus (Rusa) mariannus* ( $p < 0.001$ , horizontal rectangles).  
475 *Cervus (Rusa)* sp. (open triangles) on the other hand overlaps more with recent *Cervus (Rusa)*  
476 *unicolor* (open squares), the larger *C. unicolor* specimens from the Pleistocene Duoi Uoi (filled  
477 triangles) and fossil *C. unicolor* from Lang Trang (stars) and Tam Hang (dots). The MANOVA however  
478 suggested significant differences between *Cervus* sp. and these three forms (all  $p < 0.001$ ).

#### 479 **4.2 Geometric morphometric analysis**

480 In figure 9 the results of our metric analysis of the relative size of the anterior and posterior part of  
481 the upper molars are shown. The data point out that there was overlap between the first (green  
482 crosses) and the second molar (blue squares) and between the second- and the third molar (red  
483 crosses). Nevertheless the size difference between the anterior and posterior part was more  
484 pronounced in the third molar and therefore separated reasonably well on the y-axis. A Mann-  
485 Whitney *U*-test on the tooth index values showed the separation between m2 and m3 was  
486 statistically significant ( $p < 0.001$ ), allowing separation of the teeth. In addition to morphological  
487 criteria we identified those molars with an index of at least 120 ( $[\text{anterior width}/\text{posterior width}] \times$   
488 100) as upper M3s.

489 From our analysis in TPSSmall it can be concluded that the projection of our shape coordinates in  
490 tangent shape space is good enough for further statistical analysis (slope=0.998153 and  $p=1$ ). The  
491 repeatability test (fig. 10) revealed that although there was limited error in the digitization process,  
492 the clustering together of replicates indicates that the variation caused by digitization error was not  
493 too large to obscure natural shape variation.

494 <Fig. 9>

495 <Fig. 10>

496 A PCA of the set of 13 landmarks (fig. 11), gives limited but visual separation between certain species  
497 or groups of species. The first two components (PC1 and PC2) together explain the majority (81%) of  
498 the total variation in the dataset (table 6). The broken stick model distribution on eigenvalues  
499 suggested only the first two components were significant. Because of this reason, and because it  
500 provided the best visual separation, only the first two components were used in this analysis and  
501 visualized in figure 11. In the thin plate spline deformation grids at both ends of the two axes an idea  
502 is given of the morphological changes described by the first two components. Shape changes along  
503 the axis of PC1 can be interpreted as a change in the angle of the hypoconid relative to the  
504 protoconid. Changes along the axis of PC2 can be explained as the general development- and  
505 difference in pointiness- of the hypoconid and protoconid (fig. 11).

506 The results of a permutational MANOVA run on the scores of the relevant principle components (PC1  
507 and PC2 as indicated by a broken stick model distribution of eigenvalues) explaining together 81.1 %  
508 of the total variation, is given in table 7. Although visual separation was not clear between all groups  
509 in the initial PCA, in the permutational MANOVA the distinction was statistically significant between  
510 different clusters ( $p<0.001$ ). Non-significant differences (non-bold values in table 7) between  
511 individual species may be due to natural similarities between groups, but also because of the small  
512 sample sizes for certain taxa (*Axis lydekkeri*, *Axis kuhlii*, *Cervus mariannus* and *Cervus alfredi*) or the  
513 limited area of the teeth that was quantified.

514 To test whether the shape differences summarized in the first two components were correlated with  
515 size, the scores of PC1 and PC2 were regressed against centroid size. The results point out that there  
516 was a weak correlation between size and the first component ( $r=0,446$ ), suggesting that a small part  
517 of the shape variation in PC1 may be picking up an allometric signal. However, when removing the  
518 largest species from the sample (*Cervus unicolor*, *Elaphurus davidianus* and Sumatran *Cervus* sp.), the  
519 correlation coefficient becomes considerably smaller and negative ( $r=-0,143$ ). This suggests that if  
520 shape differences in PC1 are partially explained by allometry, these differences are primarily driven  
521 by the largest species in the sample. No significant correlation was observed between the second  
522 component and size ( $r=0,014$ ).

523 <Fig. 11>

524 <Table 6>

525 <Table 7>

526 In the PCA with all specimens included, the living members of the subgenus *Hyelaphus* (*A. kuhlii*  
527 (large crosses) and *A. porcinus* (open diamonds)) are clearly separated from recent *Axis* (*Axis*) *axis*  
528 (small crosses) on PC1 (fig. 11). The permutational MANOVA (table 7) indicates these differences are  
529 highly significant ( $p=0.0095$ ,  $p<0.001$ ). Although in the taxonomic scheme followed in this paper  
530 (Groves and Grubb 1987), *Hyelaphus* and *Axis* are placed together under the same genus (*Axis*), it is  
531 not unlikely that these scores reflect a true phylogenetic difference. As already mentioned, more  
532 recent molecular and morphological studies (Pitra *et al.* 2004, Meijaard and Groves 2004) have  
533 argued that *Hyelaphus* may not be closely related to *Axis* and should perhaps be placed closer to the  
534 subgenus *Rusa*.

535 In addition, the fossil *Axis lydekkeri* (dots) also grouped together with the two species of the  
536 subgenus *Hyelaphus* (open diamonds and large crosses) in the PCA (fig. 11). Differences between *A.*  
537 *lydekkeri*, *A. porcinus* ( $p=0.3334$ ) and *A. kuhlii* ( $p=0.4902$ ) were not significant. This is in agreement

538 with the conclusions by Meijaard and Groves (2004) that *Axis lydekkeri* should be placed under the  
539 (sub)genus *Hyelaphus* and not *Axis*. These shape differences are not thought to be size related, as no  
540 allometric effect was observed in PC1 and PC2 amongst the smaller sized species. Due to the fact that  
541 different species within the *Hyelaphus* group overlapped and because of the small sample size, it was  
542 not possible to get a better insight into the relationships between *A. lydekkeri*, *A. porcinus* and *A.*  
543 *kuhlii*.

544 Members of the subgenera *Cervus* (vertical rectangles), *Rucervus* (inversed triangles) and *Rusa*  
545 (squares, filled triangles and filled diamonds) did not separate well on PC1 (fig. 11) and, as suggested  
546 from the regressions, a limited allometric effect may be present for the larger species within these  
547 groups. There is, on the other hand, some weak separation on PC2. The proximity of these subgenera  
548 in morphospace (fig. 11) suggests a close similarity between *Cervus* s.s. and *Rusa*, which is supported  
549 by the molecular studies by Pitra *et al.* (2004). *Elaphurus davidianus* (horizontal rectangles) scores  
550 highest on PC1, but as this is the largest species in the sample, caution is urged due to the possibility  
551 of a limited allometric effect as suggested by the regressions against centroid size. Within the  
552 subgenus *Rusa* (squares, filled triangles and filled diamonds), there is overlap in the PCA (fig. 11)  
553 between all species with the exception of *Cervus (Rusa) alfredi* (filled triangles). On the vertical axis  
554 (PC2) *Cervus (Rusa) timorensis* (filled squares) scores generally higher than *Cervus (Rusa) unicolor*  
555 (open squares) but there is overlap in the center. The fossil *Cervus kendengensis* (circles) groups  
556 reasonably well with *Cervus (Rusa) timorensis* (filled squares), but also to a limited extent with *Cervus*  
557 (*Rusa*) *unicolor* (open squares). The permutational MANOVA (table 7) however pointed out that both  
558 *C. kendengensis* and *C. timorensis* are significantly different from *C. unicolor* ( $p=0.0001$ ,  $p=0.0082$ )  
559 but not from each other ( $p=0.2524$ ).

560 Although in the linear morphometric analysis (fig. 8) the Pleistocene *Cervus (Rusa)* sp. from Sumatra  
561 (open triangles) appears to be clearly larger in size than *Cervus (Rusa) timorensis* (filled squares), in  
562 the geometric morphometric analysis it overlaps with *Cervus (Rusa) timorensis* (filled squares) as well

563 as with the fossil *Cervus kendengensis* (circles) and recent *Cervus (Rusa) unicolor* (open squares). The  
564 permutational MANOVA (table 7) indicated that *Cervus* sp. is significantly different from *Cervus*  
565 *unicolor* ( $p=0.0019$ ) but not from both *Cervus timorensis* ( $p=0.5149$ ) and *Cervus kendengensis*  
566 ( $p=0.0545$ ).

567 In order to get a better separation between *Rusa* species, a Canonical Variates Analysis (CVA) was run  
568 on the first 12 components of the PCA that together summarized 99.6% of the total variance, with  
569 only *Cervus kendengensis* (dots), Pleistocene *Cervus (Rusa)* sp. from Sumatra (open triangles) and the  
570 living members of the subgenus *Rusa* (filled squares, filled triangles, open squares and ellipses)  
571 included. The results are plotted out in figure 12. Visual separation between the living species is  
572 clearly much better than in the PCA and happens mostly on the horizontal axis.

573 *Cervus kendengensis* (dots) groups closely together with *Cervus (Rusa) timorensis* (filled squares), and  
574 is further removed from the other recent species in morphospace. Contrary to what was suggested  
575 by the results of the linear morphometric analysis (fig.11), the fossil *Cervus (Rusa)* sp. from Sumatra  
576 (open triangles) clearly overlap with *Cervus (Rusa) timorensis* (filled squares) and not with any of the  
577 other living *Rusa*-deer like *Cervus (Rusa) unicolor* (open squares) or *Cervus (Rusa) alfredi* (filled  
578 triangles). If we consider the percentage of correct reclassifications for the different assigned groups  
579 in table 8(a), 42% of the specimens were correctly reclassified to the right species with jackknifed  
580 cross-validation. However, when considering *Cervus kendengensis*, *Cervus (Rusa) timorensis* and  
581 *Cervus (Rusa)* sp. as a single group (table 8b), 78% of the specimens were correctly reclassified.

582 <Fig. 12>

583 <Table 8 >

## 584 **5. Discussion and conclusions**

585 The results of the linear morphometric analysis showed considerable overlap between different  
586 species and the size range of some species may have been wider in the past than may be expected

587 from their living conspecifics. Nevertheless, some conclusions can be drawn from the results. The  
588 linear study included a broader range of fossil species than the geometric morphometric analysis, but  
589 both methods provided similar results.

590 It can be concluded from the two methods that both medium- and larger sized deer species are  
591 present in the Javanese fossil record. This confirms statements by Martin (1888) and Dubois (1891,  
592 1907, 1908) that besides *Axis lydekkeri*, there is also at least one larger form present during the  
593 Pleistocene in Java.

594 *Axis lydekkeri*, the best known species, is most similar in shape to *Axis (Hyelaphus) porcinus* and *Axis*  
595 (*Hyelaphus*) *kuhlii*. We therefore follow Meijaard and Groves (2004), in that *A. lydekkeri* should be  
596 placed under the subgenus *Hyelaphus*. The results of the geometric morphometric analysis also  
597 strongly suggest that the genus *Axis* needs revision and that extant *Axis kuhlii* and *Axis porcinus* may  
598 not be closely related to *Axis axis*. While the extinct *A. lydekkeri* and recent *A. kuhlii* and *A. porcinus*  
599 seem closely related, the relationship between these tree species individually is not clear, although  
600 linear measurements suggest it is most closely related to *A. kuhlii*. This is not unlikely since *A. kuhlii* is  
601 still present in Java.

602 The fossil *Axis* sp. from Ngebung is undoubtedly smaller in size than *Axis javanicus*, but falls within  
603 the range of *Axis lydekkeri*. Although we cannot exclude its identification as *Cervus oppenoorthi*, we  
604 provisionally place it under *Axis lydekkeri*. Contrary to von Koenigswald's (1933) statement, only  
605 slight differences in size or robustness were found between *Cervus zwaani* and *Axis lydekkeri*. The  
606 linear morphometric analysis suggested some difference between these two, but no significant  
607 difference between *C. zwaani* and the *Axis* specimens from Ngebung (who were found highly similar  
608 to *A. lydekkeri*). Based on the linear morphometric analysis and given the scant fossil evidence, *C.*  
609 *zwaani* should therefore probably be considered a junior synonym of *Axis lydekkeri*, as was suggested  
610 by Zaim *et al.* (2003).

611 *Axis javanicus* is similar in size to recent *Axis axis* and larger than *Axis kuhlii*, *Axis porcinus* and fossil  
612 *Axis lydekkeri*. We consider it a valid species, but whether its closest living relative is *Axis axis* cannot  
613 be concluded with certainty from the data. As for *Cervus oppenoorthi*, no conclusions can be drawn  
614 about its validity since it was not included in our analysis. From the literature it can be inferred that it  
615 is probably related to the *Hyelaphus*-group.

616 *Cervus problematicus* was not included in the geometric morphometric analysis, but the clear  
617 difference in size from all other known Javanese species suggests it cannot be identified as any of the  
618 other known fossil taxa. It is similar in size to the living *Cervus (Rusa) unicolor*, but in view of the fact  
619 that there are no fossil or historical records for this species in Java, we provisionally recognize *C.*  
620 *problematicus* as a valid species.

621 *Cervus (Rusa) stehlini* was considered by von Koenigswald as a separate species from *Cervus (Rusa)*  
622 *timorensis*, based on the peculiar morphology and slenderness of its premolars (von Koenigswald  
623 1933). Although the species was not included in the geometric morphometric analysis and no  
624 premolars were included in this study in general, the lower m3 was not found to be more slender  
625 than that of *C. timorensis*. Although its validity could not be refuted with certainty here, we urge for  
626 caution when attributing fossils to this taxon. If not synonymous with *C. timorensis*, it is probably  
627 closely related to it.

628 *Cervus palaeomendjangan* was not included in this study, as it is unclear what specimens Dubois  
629 (1908) was referring to when proposing it as a new species. The scant evidence in addition to von  
630 Koenigswald (1933) who considered it invalid, imply that it may be a synonym of one of the other  
631 species.

632 As Dubois (1908) already pointed out, *Cervus kendengensis* is similar in shape to *Cervus (Rusa)*  
633 *timorensis*. He considered it a separate species mainly based on the morphology of the antlers. The  
634 linear morphometric analysis confirms its placement under the subgenus *Rusa*. Moreover, the  
635 geometric morphometric analysis indicated it is more similar in morphology to *C. timorensis* than to

636 any of the other living *Rusa* deer. Awaiting further research on e.g. antler morphology we consider it  
637 a valid species, though closely related, if not ancestral to the Javanese sambar (*C. timorensis*).

638 The presence of *Cervus (Rucervus) eldii* in the Javanese Pleistocene record, though not tested in this  
639 study, is considered unlikely. No other records of this species are known from Java or the rest of  
640 Sundaland. Moreover, the supposed characteristic morphology of the antler fragment (the angle  
641 between the beam and the brown tine) is also reported for other Javanese fossil species (*Axis*  
642 *javanicus*) (von Koenigswald 1933). We regard *C. eldii* as absent from the Javanese fossil record.

643 The Sumatran Pleistocene deer (*Cervus (Rusa) sp.*) clusters with *Cervus (Rusa) unicolor* when  
644 considering size, but the geometric morphometric analysis pointed out its similarity to *Cervus (Rusa)*  
645 *timorensis* and the fossil species *Cervus kendengensis*. This is surprising, since the majority of the  
646 fauna associated with *Cervus sp.* is considered essentially modern (de Vos 1983) and *Cervus (Rusa)*  
647 *unicolor* is the only deer of the Cervini tribe currently present on Sumatra. If our identifications are  
648 sound, there are several possible scenarios for the Pleistocene deer of Sumatra. One possibility is  
649 that *Cervus (Rusa) sp.* is synonymous with *Cervus (Rusa) timorensis*, but that its size range was wider  
650 in the past. From the measurements on the mainland deer fossils it was already suggested that this  
651 was the case with *Cervus (Rusa) unicolor*. In addition, it should be noted that large sizes were also  
652 observed for several other mammal groups found in the Sumatran cave deposits, such as  
653 *Symphalangus* (Hooijer 1960), *Pongo* (Hooijer 1948, Harrison 2000) and *Hystrix* (Hooijer 1946).  
654 Although there is some debate whether these differences are enough for the recognition of separate  
655 subspecies (Badoux 1959, Van Weers 2003), it demonstrates a larger flexibility in size than what may  
656 be expected from their living representatives. Likewise, a similar size reduction since the Late  
657 Pleistocene was also observed in Borneo for a number of mammals like *Tapirus*, *Pongo*, several  
658 cercopithecids and even *Muntiacus* (Medway 1964).

659 Another possibility is that *Cervus (Rusa) unicolor* is not monospecific. According to a recent  
660 taxonomic revision by Groves (2011), the sambar should be split up in two species: *Cervus (Rusa)*

661 *unicolor* from Sri Lanka and mainland South Asia and *Cervus (Rusa) equina* from Southeast Asia and  
662 the Indomalayan archipelago. Since a large portion of our *C. unicolor* sample was not provenanced, it  
663 is possibly biased towards specimens from the Indian subcontinent (*Cervus/Rusa unicolor unicolor*). If  
664 the Indomalayan species *Cervus (Rusa) equina* is more closely related to *C. timorensis*, as proposed  
665 by Groves (2011), this would also have implications for the position of both *Cervus (Rusa)* sp. and  
666 *Cervus kendagensis* in our analysis as we would have missed a crucial species.

667 A third possibility is that the fossils from Sumatra belong to an extinct species different from both  
668 *Cervus timorensis* and *Cervus unicolor*. In that case the data still suggests that it is most closely  
669 related to *Cervus timorensis* and the fossil *Cervus kendagensis*.

## 670 **6. General conclusion**

671 This attempt to shed new light on the taxonomic relationships between the Pleistocene Cervini from  
672 Java and Sumatra, has resulted in some novel insights. Although our study was hampered by  
673 difficulties such as the inaccessibility of some material and the fact that certain species are only  
674 known from antler fragments, our results show that a combination of linear- and geometric  
675 morphometrics can be used to gain a better understanding of Southeast Asian deer taxonomy.

676 This quantitative approach was deemed especially helpful in a group of fossil mammals, where  
677 different taxa have traditionally been separated based on subtle and often subjective, qualitative  
678 criteria. However, in order to construct a more conclusive taxonomic review there are several  
679 problems to overcome. Firstly, a thorough and conclusive revision of the taxonomy and phylogeny of  
680 recent Cervini is needed, which can then be used as a reliable baseline for further paleontological  
681 research. Besides that, there is a need to apply similar methods to other deer elements and species  
682 from fossil collections in Java and Sumatra, and ideally also from the Asian mainland. This is  
683 especially the case for antlers as several Pleistocene deer have been placed in separate taxa because  
684 of their particular antler morphology. As a third note, we argue for a better understanding of body  
685 size variability in living and fossil deer and how this is reflected in tooth size.

686 Ultimately, a more complete and integrated knowledge of Southeast Asian fossil and living cervid  
687 taxonomy and evolution should lead to a better understanding of the changing environmental  
688 conditions that were present in Southeast Asia during the Quaternary. This in turn could be linked  
689 with other palaeoecological datasets and contribute to the understanding of our own genus' ecology  
690 in Eurasia during the Pleistocene and Holocene.

## 691 **Acknowledgements**

692 The authors would like to thank the curators and collection managers who facilitated our data  
693 collection: Reinier van Zelst, Henry van der Es, Andrew Kitchener, Zena Floody, Joséphine Lesur,  
694 George Lenglet, Sebastien Bruaux, Dominique Verschelde, Daniela Kalthoff, Marjan Doom, Fachroel  
695 Aziz and Andy Currant. Our gratitude also goes to Tarek Oueslati, Una Strand-Vidarsdottir and Sarah  
696 Elton for their insights and to the reviewers for their helpful comments. We are especially grateful to  
697 Anne Marie Bacon, Vu The Long, Nguyen Thi Kim Thu and Thongsa Sayavongkhamdy for providing us  
698 with the measurements from Duoi U'oi and Tam Hang.

699

## 700 **Figures**

701 *Fig. 1: map of Sundaland during the last glacial maximum (adapted from Bird et al. 2005)*

702 *Fig. 2: Map of Asia with distribution of recent Cervini included in this analysis. The Western*  
703 *distribution of red deer (*Cervus elaphus*) in North Africa, Europe and North America and that of fallow*  
704 *deer (*Dama dama*) in Europe, is not illustrated. (1=*Dama dama*, 2=*Elaphurus davidianus*, 3=*Axis axis*,*  
705 *4=*Cervus alfredi*, 5=*Axis kuhlii*, 6=*Cervus timorensis*, 7=*Cervus unicolor*, 8=*Cervus elaphus*, 9=*Rucervus**  
706 *eldii*, 10=*Axis porcinus*, 11=*Rucervus duvaucelli*, 12=*Cervus mariannus*, 13=*Axis calamianensis*).  
707 *Species distributions are based on van Bemmelen (1949), Corbet (1978), Chapman and Chapman (1980),*  
708 *Groves (1982), Cao (1993) and Grubb (2005)*

709 Fig. 3: Anterior width (AW) and posterior width (PW) measurements on the upper M3, adapted from  
710 Lister (1996).

711 Fig. 4: Positioning of landmarks on the upper third molar. I to IV are type 2 landmarks, 'a' to 'i' are  
712 type 3 landmarks.

713 Fig. 5: Length and width measurements of fossil lower m3s from Java. "f"= fossil  
714 *C.hippelaphus/timorensis*

715 Fig. 6: Length and width measurements of Javanese fossil- and recent lower m3s of the (supposed)  
716 subgenus *Rusa*. "f"= fossil *C.hippelaphus/timorensis*

717 Fig. 7: Length and width measurements of fossil and modern lower m3s of the (supposed) genus *Axis*.

718 Fig. 8: Length and width measurements of lower m3s of extant members of the subgenus *Rusa*, fossil  
719 *Cervus (Rusa) unicolor* from mainland Southeast Asia and fossil *Cervus (Rusa) sp.* from Sumatra.

720 Fig. 9: Ratio of the relative width of the anterior and posterior part of the upper M3 against molar  
721 length for recent specimens (AW=anterior width; PW= posterior width)

722 Fig. 10: results on PC1 and PC2 of PCA repeatability test on random specimens (1 specimen=1  
723 color/symbol)

724 Fig. 11: PCA of all deer teeth (first two components). Shape changes along the axes of PC1 and PC2  
725 are visualized with thin plate spline deformation grids showing hypothetical extreme values at the  
726 end of each axis.

727 Fig. 12: CVA of first twelve principle components for *Cervus kendengensis*, *Cervus (Rusa) timorensis*,  
728 Sumatran *Cervus (Rusa) sp.*, *Cervus (Rusa) mariannus*, *Cervus (Rusa) unicolor* and *Cervus (Rusa)*  
729 *alfredi*.

730

731 **Tables**

732 *Table 1: Taxonomic scheme used in this paper, based on Groves and Grubb (1987)*

733 *Table 2: Taxa known from the Javanese Pleistocene*

734 *Table 3: Fossil species included in our analysis and hypotheses that were tested.*

735 *Table 4: Overview of species used in morphometric analysis.*

736 *Table 5: p-values of MANOVA on length and width measurements of the m3, with significant values*  
737 *( $p < 0.05$ ) in bold (C. problematicus excluded as N=1).*

738 *Table 6: Variance explained by principle components 1 to 26.*

739 *Table 7: p-values of permutational MANOVA of the first two principle component scores, with*  
740 *significant values ( $p < 0.05$ ) in bold.*

741 *Table 8(a and b): Cross-validation results for the CVA on (supposed) Rusa-members with number of*  
742 *reclassifications and reclassification percentages in parenthesis. Lower table with C. kendengensis,*  
743 *Cervus (Rusa) sp. and Cervus (Rusa) timorensis as one group.*

744

745 **Bibliography**

746 Adriaens, P. 2007, *Protocol for error testing in landmark based geometric morphometrics*,  
747 unpublished document consulted on 19/12/13 at: [http://www.funmorph.ugent.be/Miscel/](http://www.funmorph.ugent.be/Miscel/Methodology/Morphometrics.pdf)  
748 [Methodology/Morphometrics.pdf](http://www.funmorph.ugent.be/Miscel/Methodology/Morphometrics.pdf)

749 Albarella, U. 2009, Size and shape of the Eurasian wild boar (*Sus scrofa*), with a view to the  
750 reconstruction of its Holocene history, *Environmental Archaeology*, 14, pp. 103-136.

751 Auetrakulvit, P. 2004, *Faunes du Pléistocène final à l'Holocène de Thaïlande : approche*  
752 *archéozoologique*. PhD dissertation University of Aix-Marseille I.

753

754 Aziz, F. & de Vos, J. 1999, The fossil faunas from Citarum Area, West Java, Indonesia, In: Reumer,  
755 J.W.F. & de Vos, J. (eds), Elephants have a snorkel!, Papers in honour of Paul Y. Sondaar, *Deinsea*, 7,  
756 pp. 21-32.

757

758 Bacon, A. M., Demeter, F., Tougard, C., de Vos, J., Sayavongkhamdy, T., Antoine, P.O.,  
759 Bouasisengpaseuth, B. & Sichanthongtip, P. 2008, Redécouverte d'une faune pléistocène dans les  
760 remplissages karstiques de Tam Hang au Laos : Premiers resultats, *Comptes Rendus Palevol*, 7,  
761 pp.277-288.

762

763 Bacon, A.M., Demeter, F., Duringer, P., Helm, C., Bano, M., Long, V.T., Thuy, N.T., Antoine, P.O., Mai,  
764 B.T., Huong, N.T.M, Dodo, Y., Chabaux, F. & Rihs, S. 2008b, The Late Pleistocene Duoi U'Oi cave in  
765 Northern Vietnam: palaeontology, sedimentology, taphonomy and palaeoenvironments, *Quaternary*  
766 *Science Reviews*, 27, pp. 1627-1654.

767

768 Baab, K., McNulty, K. & Rohlf, F. 2012, The shape of human evolution: a geometric morphometrics  
769 perspective, *Evolutionary Anthropology*, 21, pp. 151-165.

770

771 Bacon, A. M., Demeter, F., Duringer, P., Helm, C., Bano, M., Long, V. T., Thuy, N. T. K., Antoine, P.-O.,  
772 Mai, B. T., Huong, N. T. M., Dodo, Y., Chabaux, F. & Rihs, S. 2008, The Late Pleistocene Duoi U'Oi cave  
773 in northern Vietnam: palaeontology, sedimentology, taphonomy and palaeoenvironments  
774 *Quaternary Science Reviews*, 27, pp. 1627-1654.

775

776 Badoux, D.M. 1959, *Fossil mammals from two fissur deposits at Punung (Java)*, PhD dissertation  
777 Universiteit Utrecht.

778

779 van Bemmelen, A. C. 1944, The taxonomic position of *Cervus kuhlii* Müll. et Schl., *Treubia*, 1, pp. 149–  
780 155.  
781

782 van Bemmelen, A.C. 1949, Revision of the Rusine deer in the Indo-Australian archipelago, *Treubia*, 20,  
783 2, pp. 191-262.  
784

785 van den Bergh, G. D., De Vos, J. & Sondaar, P. Y. 2001, The Late Quaternary palaeogeography of  
786 mammal evolution in the Indonesian Archipelago, *Palaeogeography, Palaeoclimatology,*  
787 *Palaeoecology*, 171, pp. 385-408.  
788

789 Bland, J. M., and Altman, D. G. 1986, Statistical methods for assessing agreement between two  
790 methods of clinical measurement, *Lancet* i, pp. 307–310.  
791

792 Bookstein, F.L. 1997, Landmark methods for forms without landmarks: morphometrics of group  
793 differences in outline shape, *Medical Image Analysis*, 1, pp. 225.  
794

795 Bouteaux, A. 2005, *Paléontologie, Paléoécologie et Taphonomie des mammifères du Pléistocène*  
796 *moyen ancien du site à hominidés de Sangiran (Java Central, Indonésie)*, PhD dissertation Muséum  
797 National d'Histoire Naturelle de Paris.  
798

799 van den Brink, L.M. 1982, On the mammal fauna of the Wajak Cave, Java (Indonesia), *Modern*  
800 *Quaternary Research in Southeast Asia*, 7, pp. 177-193.

801 van den Brink, L.M. 1983, On the vertebrate fauna of the Goea Djimbe Cave, West Java (Indonesia),  
802 Unpublished report National Museum of Natural History, Leiden, pp. 1-25.

803 Brophy, J. K., de Ruiter, D. J., Athreya, S. & DeWitt, T. J. 2014, Quantitative morphological analysis of  
804 bovid teeth and implications for paleoenvironmental reconstruction of Plovers Lake, Gauteng  
805 Province, South Africa, *Journal of Archaeological Science*, 41, pp. 376-388.

806

807 Cao, K. 1993, Selection of a suitable area for reintroduction of wild Pere David's in China, In: Ohtaishi,  
808 N. and Sheng, H.I. (eds), *Deer of China: Biology and Management*, pp. 297–300.

809

810 Castaños, J., Castaños, P. & Murelaga, X. 2006, Estudio osteométrico preliminar de los restos de  
811 ciervo (*Cervus elaphus*) del yacimiento paleontológico del Pleistoceno Superior de Kiputz IX (Mutriku,  
812 Gipuzkoa), *Geogaceta*, 40, pp. 163-166.

813 Castaños, J., Castaños, P., Murelaga, X., Alonsoolazabal, A., Ortega, L. A. & Zuluaga, M.C. 2012,  
814 Osteometric analysis of scapula and humerus for *Rangifer tarandus* and *Cervus elaphus*: A  
815 contribution to cervid discrimination (Late Pleistocene, Southern Pyrenees), *Acta Palaeontologica*  
816 *Polonica*, 5, pp. 1-18.

817

818 Chapman, N. G. & Chapman, D. I. 1980, The distribution of fallow deer: a worldwide review, *Mammal*  
819 *Review*, 10, pp. 61-138.

820

821 Corbet, G. B. 1978, *The Mammals of the Palaearctic Region: a Taxonomic Review*, British Museum  
822 (Natural History) and Cornell University Press, London, UK and Ithaca, NY, USA.

823

824 Cucchi, T., Fujita, M., Dobney, K. 2009, New insights into pig taxonomy, domestication and human  
825 dispersal in Island South East Asia: molar shape analysis of *Sus* remains from Niah caves, Sarawak,  
826 *International Journal of Osteoarchaeology*, 19, pp. 508-530.

827

828 Cucchi, T., Hulme-Beaman, A., Yuan, J. & Dobney, K. 2011, Early Neolithic pig domestication at Jiahu,  
829 Henan Province, China: clues from molar shape analyses using geometric morphometric approaches,  
830 *Journal of Archaeological Science*, 38, pp. 11-22.

831

832 Curran, S. 2009, *Hominin Paleoecology and Cervid Ecomorphology*, PhD dissertation University of  
833 Minnesota.

834 Dammerman, K.W. 1934, On prehistoric mammals from the Sampoeng Cave, Central Java, *Treubia*,  
835 14, pp. 477-486.

836 Degerbol, M. 1963, Prehistoric cattle in Denmark and adjacent areas, In: Mourant A. & Zeuner F.  
837 (eds.), *Man and cattle*, London, Royal Anthropological Institute, pp. 69–79.

838

839 Degusta, D. & Vrba, E. 2005, Methods for inferring paleohabitats from discrete traits of the bovid  
840 postcranial skeleton, *Journal of Archaeological Science*, 32, pp. 1115-1123.

841 Di Stefano, G. & Petronio, C. 2002, Systematics and evolution of the Eurasian Plio-Pleistocene tribe  
842 Cervini (Artiodactyla, Mammalia). *Geol. Rom.*, 36, pp. 311–334.

843

844 Dubois, E. 1891, Voorloopig bericht omtrent het onderzoek naar de Pleistocene en Tertiaire  
845 vertebraten-fauna van Sumatra en Java, gedurende het jaar 1890, *Natuurkundig Tijdschrift voor*  
846 *Nederlandsch-Indië*, 51, pp. 93-100.

847

848 Dubois, E. 1907, Eenige van Nederlandschen kant verkregen uitkomsten met betrekking tot de kennis  
849 der Kendeng-fauna (fauna van Trinil), *Tijdschrift Koninklijk Nederlandsch Aardrijkskundig*  
850 *Genootschap Series*, 2, 24, pp. 449 – 458.

851 Dubois, E. 1908, Das geologische Alter de Kendengoder Trinil Fauna, *Tijdschrift van het Koninklijk*  
852 *Nederlands Aardrijkskundig Genootschap*, 25, pp. 1235-1270.

853 Emerson, B. C. & Tate, M. L. 1993, Genetic analysis of evolutionary relationships among deer, *J.*  
854 *Hered.*, 84, p. 266–273.

855

856 Evin, A., Cucchi, T., Cardini, A., Vidarsdottir, U. S., Larson, G. & Dobney, K. 2013, The long and winding  
857 road: identifying pig domestication through molar size and shape, *Journal of Archaeological Science*,  
858 40, pp. 735-743.

859

860 Evin, A., Dobney, K., Schafberg, R., Owen, J., Vidarsdottir, U. S., Larsone, G. & Cucchi, T. 2013,  
861 Contrasting the effects of natural and artificial selection on the dentition of West Palearctic *Sus scrofa*,  
862 *Journal of Evolutionary Biology*, 40, pp. 1-29.

863

864 Fox, R. 1970, The Tabon Caves, Unpublished report at the National Museum of the Philippines,  
865 Manila.

866

867 Geist, V. 1998, *Deer of the world. Their evolution, behaviour, and Ecology*, Stackpole Books,  
868 Mechanicsburg.

869

870 Goodall, C. 1991, Procrustes Methods in the Statistical Analysis of Shape, *Journal of the Royal*  
871 *Statistical Society*, 53, 2, pp. 285-339.

872

873 Groves, C. P. 1982, Geographic variation in the Barasingha or Swamp Deer (*Cervus duvauceli*), *Journal*  
874 *of the Bombay Natural History Society* ,79, pp. 620–629.

875

876 Groves, C.P. & Grubb, P. 1987, Relationships of living deer. In: Wemmer, C.M. (Ed.), *Biology and*  
877 *Management of the Cervidae*, Smithsonian Inst. Press, Washington, DC.

878

879 Groves, C. 2007, Family Cervidae, In: Protheroe, D.R. & Ross, S.E. (eds.), *The Evolution of Artiodactyls*,  
880 Johns Hopkins University Press, Baltimore, pp. 249-256.

881

882 Grubb, P. 2005, Artiodactyla, In: Wilson, D.E. & Reeder, D.M. (eds), *Mammal Species of the World. A*  
883 *Taxonomic and Geographic Reference (3rd ed)*, Johns Hopkins University Press, Baltimore, USA, pp.  
884 637-722.

885

886 Harrison, T. 1998, Vertebrate faunal remains from Madai cave (MAD 1/28), Sabah, East Malaysia,  
887 *Indo-Pacific Prehistory Association Bulletin*, 17, pp. 85-92.

888

889 Harrison, T. 2000, Archaeological and ecological implications of the primate fauna from prehistoric  
890 sites in borneo, *Indo-Pacific Prehistory Association Bulletin* , 20, pp. 133-146.

891

892 Harrison, T., Krigbaum, J. & Manser, J., Lehman, S. & Fleagle, J. 2006, Primate biogeography and  
893 ecology of the Sunda Shelf Islands: a paleontological and zooarchaeological perspective, In: Lehman,  
894 S.E. & Fleagle, J.F. (Eds.), *Primate biogeography*, Springer, New York, pp. 332-372.

895

896 Hedges, S., Duckworth, J.W., Timmins, R.J., Semiadi, G. & Priyono, A. 2008, *Rusa timorensis*, In: IUCN  
897 2013. IUCN Red List of Threatened Species. Version 2013.1. <[www.iucnredlist.org](http://www.iucnredlist.org)>. Downloaded on  
898 21 October 2013.

899 Heintz, E. 1970, Les cervidés villafranchiens de France et d'Espagne, *Memoires du Muséum National*  
900 *d'Histoire Naturelle serie C. Sciences de Terre*, 22, 1 & 2, pp. 206-303.

901

902 Hooijer, D.A. 1946, Some remarks on recent, prehistoric, and fossil porcupines from the Malay  
903 Archipelago, *Zoologische Mededelingen*, 26, pp. 251-267.

904

905 Hooijer, D. 1948, Prehistoric teeth of man and of the orang-utan from central Sumatra, with notes on  
906 the fossil orang-utan from Java and Southern China, *Zoologische Verhandelingen Museum Leiden*, 29,  
907 pp. 175-293.

908

909 Hooijer, D.A. 1955, Fossil Proboscidea from the Malay archipelago and the Punjab, *Zoologische*  
910 *Verhandelingen*, 28, pp.1-163.

911

912 Hooijer, D. 1960, Quaternary gibbons from the Malay archipelago, *Zoologische Verhandelingen*  
913 *Museum Leiden*, 46, pp. 1-42.

914

915 Hooijer, D. 1962, Report upon a collection of Pleistocene mammals from tin-bearing deposits in a  
916 limestone cave near Ipoh, Kintah Valley, Perak, *Federation Museums Journal*, 7, pp. 1-5.

917

918 Ibrahim, Y. K., Peng, L. C., of Cranbrook, E. & Tshen, L. T. 2012, Preliminary report on vertebrate  
919 fossils from Cistern and Swamp Caves at Batu Caves near Kuala Lumpur, *Bulletin of the Geological*  
920 *Society of Malaysia*, 58, pp. 1-8.

921

922 Indriati, E., Swisher, C.C., Lepre, C., Quinn, R., Suriyanto, R.A., Hascaryo, A.T., Gru, R., Feible, C.S.,  
923 Pobiner, B., Aubert, M., Lees, W. & Anton, S.C. 2011, The age of the 20 meter Solo river terrace, Java,  
924 Indonesia and the survival of *Homo erectus* in Asia, *Plos One*, 6, pp. 1-10.

925

926 Kaifu, Y., Baba, H., Aziz, F., Endriati, E., Schrenk, F. & Jacob, T. 2005, Taxonomic affinities and  
927 evolutionary history of the early Pleistocene hominids of Java: dentognathic evidence, *American*  
928 *Journal of Physical Anthropology*, 128, pp. 709-726.

929

930 von Koenigswald, G.H.R. 1933, Beitrag zur Kenntnis der fossilen Wirbeltiere Javas I. Teil,  
931 *Wetenschappelijke Mededeelingen Dienst Mijnbouw Nederlandsch-Indië*, 23, pp. 1-127.

932

933 von Koenigswald, G.H.R. 1934, Zur stratigraphie des javanischen Pleistocän, *De*  
934 *ingenieur in Nederlandsch-Indië*, 1, 4, pp. 185-201.

935 von Koenigswald, G.H.R. 1935, Die fossilen Säugetierfaunen Javas, *Proceedings Koninklijke*  
936 *Nederlandse Akademie van Wetenschappen*, 38, pp. 88-98.

937

938 Kusatman, B. 1991, *The Origins of Pig Domestication with Particular Reference to the Near East*, PhD  
939 dissertation University of London.

940

941 Liouville, M. 2007, *Variabilité du Cerf elaphe (Cervus elaphus L. 1758) au cours du Pléistocène Moyen*  
942 *et Supérieur en Europe occidentale: approches morphométrique, paléoécologique et cynégétique*,  
943 PhD dissertation Muséum National d'Histoire Naturelle de Paris.

944

945 Lister, A., Parfitt, S., Owen, F., Collinge, S. & Breda, M. 2010, Metric analysis of ungulate mammals in  
946 the early Middle Pleistocene of Britain in relation to taxonomy and biostratigraphy II: Cervidae,  
947 Equidae and Suidae, *Quaternary International*, 228, pp. 157-179.

948

949 Long, V. T., de Vos, J. & Ciochon, R. 1996, The fossil mammal fauna of the Lang Trang caves, Vietnam,  
950 compared with Southeast Asian fossil and recent mammal faunas: the geographical implications,  
951 *Indo-Pacific Prehistory Association Bulletin*, 14, pp. 101-109.

952

953 Louys, J., Curnoe, D. & Tong, H. 2007, Characteristics of Pleistocene megafauna extinctions in  
954 Southeast Asia, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 243, pp. 152-173.  
955

956 Martin, K. 1888, Neue Wirbelthierreste vom Pati-Ajam auf Java - Leiden, *Sammlungen des*  
957 *geologischen Reichs-Museums*, 4, pp. 87-116.

958

959 Medway, L. 1964, Post-Pleistocene changes in the mammalian fauna of Borneo, *Studies in*  
960 *Speleology*, 1, pp. 33-37.

961

962 Meijaard, E. & Groves, C. 2004, Morphometrical relationships between South-East Asian deer  
963 (Cervidae, tribe Cervini): evolutionary and biogeographic implications, *Journal of Zoology*, 263, pp.  
964 179-196.

965

966 Moigne, A., Awe, R., Sémah, F. & Sémah, A. 2004, The cervids from the Ngebung site (Kabuh series,  
967 Sangiran Dome, Central Java) and their biostratigraphical significance, *Modern Quaternary research*  
968 *in Southeast Asia*, 18, pp. 31-44.

969

970 Moigne, A.; Sémah, F.; Sémah, A.; Bouteaux, A. & Awe, R. D. 2004, Mammalian fossils from two sites  
971 of the Sangiran dome (Central Jawa, Indonesia), in the bio-stratigraphical framework of the Jawanese  
972 Pleistocene, *Proceeding of the 18th international Senckenberg Conference 2004 in Weimar*, pp. 1-3.

973

974 O'Regan, H. & Kitchener, A.C. 2005, The effects of captivity on the morphology of captive,  
975 domesticated and feral mammals, *Mammal Review*, 35, 3/4, pp. 215-230.

976 Payne, S. & Bull, G. 1988, Components of variation in measurements of pig bones and teeth and the  
977 use of measurements to distinguish wild from domestic pig remains, *Archaeozoologia*, 2, pp. 27-65.

978

979 Piper, P., Ochoa, J., Robles, E. C., Lewis, H. & Paz, V. 2011, Palaeozoology of Palawan Island,  
980 Philippines, *Quaternary International*, 233, pp. 142-158.  
981

982 Piper, P., Rabett, R. & Bin Kurui, E. 2008, Using community, composition and structural variation in  
983 terminal Pleistocene vertebrate assemblages to identify human hunting behaviour at the Niah caves,  
984 Borneo, *Indo-Pacific Prehistory Association Bulletin*, 28, pp. 88-98.  
985

986 Pitra, C., Fickel, J., Meijaard, E. & Groves, P. 2004, Evolution and phylogeny of old world deer,  
987 *Molecular Phylogenetics and Evolution*, 33, pp. 880-895.  
988

989 Polaszek, A., Agosti, D., Alonso-Zarazaga, M., Beccaloni, G., Bjørn, P.d.P., Bouchet, P., Brothers, D.J.,  
990 Cranbrook, G., Evenhuis, N.L., Godfray, H.C.J., Johnson, N.F., Krell, F.-T., Lipscomb, D., Lyal, C.H.C.,  
991 Mace, G.M., Mawatari, S., Miller, S.E., Minelli, A., Morris, S., Ng, P.K.L., Patterson, D.J., Pyle, R.L.,  
992 Robinson, N.J., Rogo, L., Taverne, J., Thompson, F.C., Tol, J. van, Wheeler, Q.D. & Wilson, E.O.  
993 2005, A universal register for animal names, *Nature*, 437, pp. 477.  
994  
995

996 Randi, E., Mucci, N., Pierpaoli, M. & Douzery, E. 1998, New phylogenetic perspectives in the Cervidae  
997 (Artiodactyla) are provided by the mitochondrial cytochrome *b* gene, *Proc. R. Soc. Lond.*, 265, pp.  
998 793–801.  
999

1000 Reis, K. & Garong, A. 2001, Late Quaternary vertebrates from Palawan Island, Phillipines,  
1001 *Paleogeography, Paleoclimatology, Paleoecology*, 171, pp. 409-421.  
1002

1003 Rohlf, F.J. 2003, TpsSmall, 1.20 ed., *Ecology & Evolution*, State University at Stony  
1004 Brook, New York.

1005 Rohlf, F.J., 2004, TpsDig 1.40-Thin Plate Spline Digitizer, 1.40 ed., *Ecology & Evolution*,  
1006 State University at Stony Brook, New York.  
1007  
1008 Rohlf, F.J., 2005, TpsRelw 1.41-Thin plate Spline Relative Warp, 1.41 ed., *Ecology &*  
1009 *Evolution*, State University at Stony Brook, New York.  
1010  
1011 Sheets, H.D., Keonho K. & Mitchell C.E. 2004, A combined landmark and outline-based approach to  
1012 ontogenetic shape change in the Ordovician Trilobite *Triarthrus becki*, In: Elewa, A. (Ed), *Applications*  
1013 *of Morphometrics in Paleontology and Biology*, Springer, New York, pp. 67–81.  
1014  
1015 Stehlin, H.G. 1925, Fossile Säugetiere aus der Gegend von Limbangan (Java), *Wetenschappelijke*  
1016 *Mededeelingen Dienst mijnbouw Nederlandsche-Indië*, 3, pp. 1-10.  
1017  
1018 Stehn, C.E., & J.H.F. Umgrove 1929, Bijdrage tot de geologie der vlakke van Bandoeng, *Tijdschrift*  
1019 *Koninklijk Nederlandsch Aardrijkskundig Genootschap*, 46, pp. 301 – 314.  
1020  
1021 Storm, P. 1990, Newly described Neolithic site from Java. The archaeological site Hoekgrot: human  
1022 remains, artifacts and the subrecent fauna of Java, Unpublished report at the National Museum of  
1023 Natural History, Leiden, pp. 1-120.  
1024  
1025 Storm, P. 1995, The Evolutionary Significance of the Wadjak Skulls, *Scripta Geological*, 110, pp. 1-248.  
1026  
1027 Storm, P. & de Vos, J. 2006, Rediscovery of the Late Pleistocene Punung hominin sites and the  
1028 discovery of a new site Gunung Dawung in East Java, *Senckenbergiana Lethaea*, 86, pp. 271-281.  
1029  
1030 Storm, P., Wood, R. , Stringer, C., Bartsiakos, A., de Vos, J., Aubert, M., Kinsley, L. & Grün, R. 2013, U-  
1031 series and radiocarbon analyses of human and faunal remains from Wajak, Indonesia, *Journal of*  
1032 *Human Evolution*, 64, pp. 356-365.

- 1030
- 1031 Stremme, H. 1911, Die Säugetiere mit Ausnahme der Proboscidier, In: Selenka, M.L. &  
1032 Blanckenhorn, M. (eds), *Die Pithecanthropus- Schichten auf Java: Geologische und paläontologische*  
1033 *Ergebnisse der Trinil-Expedition (1907 und 1908)*, Engelmann, Leipzig, pp. 82-160.
- 1034 De Terra, H. 1941, Pleistocene formations and stone age man in China, *Publ. Inst. Géol.-Biol. Peiping*,  
1035 6, pp. 1-54.
- 1036 De Terra, H. & Patterson, T. 1939, Studies on the ice-age in India and associated human cultures,  
1037 *Carnegie Magazine*, 493, pp. 1-354.
- 1038 Viscosi, V. & Cardini, A. 2011, Leaf morphology, taxonomy and geometric morphometrics: a  
1039 simplified protocol for beginners, *Plos ONE*, 6, pp. 1-20.
- 1040
- 1041 Vogel von Falckenstein, K. 1910, *Artbestimmung der Cervus lydekkeri mart durch geweihmessung*,  
1042 n.p.
- 1043 Voris, H.K., 2000, Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time  
1044 durations, *Journal of Biogeography*, 27, pp. 1153-1167.
- 1045 de Vos, J. & Sondaar, Y. 1982, The importance of the Dubois Collection reconsidered, *Modern*  
1046 *Quaternary Research SE Asia*, 7, pp. 35-63.
- 1047 de Vos, J. 1983, The Pongo faunas from Java and Sumatra and their significance for bio-stratigraphical  
1048 and paleo-ecological interpretations, *Proc. Koninklijke Nederlandse Akadademie van Wetenschappen*,  
1049 86, pp. 417-425.
- 1050 de Vos, J. 1985, Faunal stratigraphy and correlation of the Indonesian Hominid sites, In: Delson, E.  
1051 (ed), *Ancestors: the hard evidence*, Liss, New York, pp. 215-220.

1052 de Vos, J. 2004, The Dubois collection: a new look at an old collection, In: Winkler-Prins, C. &  
1053 Donovan, S. (eds.), *Cultural Heritage in Geosciences, Mining and Metallurgy: Libraries- Archives -*  
1054 *Museums', Museums and their collections, Scripta Geologica (Special issue)*, VII International  
1055 Symposium Leiden, The Netherlands.

1056 Walker J. A. 2000, The ability of geometric morphometric methods to estimate a known covariance  
1057 matrix, *Syst. Biol.*, 49, pp. 686-696.

1058

1059 van Weers, D. 2003, The porcupine *Hystrix (Acanthion) brachyura punungensis* subsp. nov. from Late  
1060 Pleistocene fissure deposits near Punung, Java, *Scripta Geologica*, 126, pp. 217-225.

1061

1062 Westaway, K., Morwood, M., Roberts, R., Rokus, A., Zhao, J.X. & Storm, P. 2007, Age and  
1063 biostratigraphic significance of the Punung Rainforest Fauna, East Java, Indonesia, and implications  
1064 for Pongo and Homo, *Journal of Human Evolution*, 53, pp. 709-717.

1065

1066 Zaim, Y., de Vos, J., Huffman, F., Aziz, F., Kappelman, J. & Rizal, Y. 2003, A new antler specimen from  
1067 the 1936 Perring hominid site (East Jawa), Indonesia, attributable to *Axis lydekkeri* (Martin, 1886),  
1068 *Journal of Mineral Technology*, 10, pp. 1-9.

1069

1070 Zeitoun, V., Seveau, A., Forestier, H., Thomas, H., Lenoble, A., Laudet, F., Antoine, P.-O., Debruyne, R.,  
1071 Ginsburg, L., Mein, P., Winayalai, C., Chumdee, N., Doyasa, T., Kijngam, A. & Nakbunlung, S. 2005,  
1072 Découverte d'un assemblage faunique à Stegodon–Ailuropoda dans une grotte du Nord de la  
1073 Thaïlande (Ban Fa Suai, Chiang Dao), *Comptes Rendus Palevol.*, 4, pp. 255-264.

1074

1075 Zelditch, M.L., Swiderski, D.L., Sheets, H.D. & Fink, W.L. 2004, *Geometric morphometrics for*  
1076 *biologists: a primer*, Elsevier, Berlin.

Table 1  
[Click here to download high resolution image](#)

Genus	Species	Included/ not included in this analysis	Subgenus	Comments
Genus Axis	Chital ( <i>Axis axis</i> )	Included	Axis	The subgenus <i>Axis</i> consists of only one species ( <i>A. Axis</i> ) and the subgenus <i>Hyalophus</i> of three ( <i>A. kuhlii</i> , <i>A. colomianensis</i> and <i>A. porcinus</i> ). Morphological (Meijaard & Groves 2004) and molecular research (Pitra et al. 2004) support a relationship between the members of <i>Hyalophus</i> , but <i>Axis axis</i> may not be closely related to this subgenus (Meijaard & Groves 2004).
	Bawean deer ( <i>Axis kuhlii</i> )	Included	<i>Hyalophus</i>	
	Calamian deer ( <i>Axis colomianensis</i> )	Not included	<i>Hyalophus</i>	
	Hog deer ( <i>Axis porcinus</i> )	Included	<i>Hyalophus</i>	
Genus Dama	Fallow deer ( <i>Dama dama</i> )	Included	<i>Dama</i>	The divergence of <i>Dama</i> , <i>Axis</i> and <i>Cervus</i> is not well known. Emmerson & Tate (1993) suggest a close relationship with <i>Axis axis</i> , while Di stephano & Petronio (2002) argue for a Pleistocene split from the <i>Cervus-Rusa</i> lineage. According to some authors (Groves 2007) the subspecies <i>D. dama mesopotamica</i> should be considered a distinct species.
Genus Cervus	Red deer ( <i>Cervus elaphus</i> )	Included	<i>Cervus</i>	According to the molecular study by Pitra et al. (2004) <i>Cervus elaphus</i> may not be monophyletic. The Central Asian- and the North African red deer should possibly be regarded as separate species, while the Central- and East Asian group is placed together with the North American wapiti under the species <i>Cervus canadensis</i> .
	Sika deer ( <i>Cervus nippon</i> )	Not included	<i>Cervus</i>	Sika might be closely related to the East Asian red deer/wapiti (Pitra et al. 2004)
	White-lipped deer ( <i>Cervus albinotris</i> )	Not included	<i>Przewalskium</i>	White-lipped deer may be a sister species to the Wapiti/Shou/Sika group (Pitra et al. 2004)
	Eld's deer ( <i>Cervus eldi</i> )	Included	<i>Rucervus</i>	While tentatively placed under the subgenus <i>Rucervus</i> , both molecular (Pitra et al. 2004) and morphological data (Groves 2007) suggest a separate genus: <i>Panolia</i> .
	Barasingha ( <i>Cervus duvauceli</i> )	Included	<i>Rucervus</i>	Molecular data (Pitra et al. 2004) suggests <i>C. duvauceli</i> and <i>C. Schomburgki</i> are most closely related to <i>Axis axis</i> , but differences are large enough to retain two separate genera ( <i>Axis</i> and <i>Rucervus</i> )
	Schomburgk's deer ( <i>Cervus schomburgki</i> )	Not included	<i>Rucervus</i>	
	Sambar ( <i>Cervus unicolor</i> )	Included	<i>Rusa</i>	<i>Cervus timorensis</i> and <i>Cervus unicolor</i> may be closely related to the subgenus <i>Hyalophus</i> (Pitra et al. 2004)
	Javan rusa ( <i>Cervus timorensis</i> )	Included	<i>Rusa</i>	
	Philippine spotted deer ( <i>Cervus ofredi</i> )	Included	<i>Rusa</i>	Cranio-metric research suggests a similarity between <i>Cervus ofredi</i> and <i>Cervus mariannus</i> but both may be distinct from <i>Cervus timorensis</i> and <i>Cervus unicolor</i> (Meijaard & Groves 2004).
	Philippine deer ( <i>Cervus mariannus</i> )	Included	<i>Rusa</i>	
Genus <i>Elaphurus</i>	Père David's deer ( <i>Elaphurus davidianus</i> )	Included	<i>Elaphurus</i>	Morphological- (Meijaard & Groves 2004) and molecular data (Pitra et al. 2004) support a separate genus, but the identity of its closest relatives remains uncertain. Possibly this species resulted from hybridisation between two species (Groves & Grubb 1987). Others argue for a fusion of the [sub-]genus with <i>Rucervus</i> (Randi et al. 2001)

Table 2  
[Click here to download high resolution image](#)

Species	Synonyms
<i>Axis Lydekkeri</i> (Martin 1886)	<i>Cervus lydekkeri</i> (Martin 1886, Vogel von Falkenstein 1910) <i>Axis axis</i> (Dubois 1891) <i>Cervus liriocerus</i> (Dubois 1907, 1908) <i>Cervus (Axis) lydekkeri</i> (Stremme 1911, Stehlin 1925, Von Koenigswald 1933, 1934)
<i>Axis javanicus</i> (Von Koenigswald 1933)	<i>Cervus javanicus</i> (Von Koenigswald 1933,1934) <i>Axis sunda</i> (Kretzoi 1947)
<i>Axis (Hyelaphus) kuhlii</i> (Temminck 1836)	<i>Cervus kuhlii</i> (Haltenorth 1963)
<i>Cervus zwoani</i> (Von Koenigswald 1933)	Possibly junior synonym of <i>Axis lydekkeri</i> (Martin 1886)
<i>Cervus (Rusa) stehlini</i> (Von Koenigswald 1933)	None known
<i>Cervus oppenoorthi</i> (von Koenigswald 1933)	According to Van Bemmelen (1944) a junior synonym of <i>Axis (Hyelaphus) kuhlii</i>
<i>Cervus (Rusa) timorensis</i> (de Blainville 1822)	<i>Cervus hippelaphus</i> <i>Cervus russa</i> <i>Cervus unicolor russa</i>
<i>Cervus kendengensis</i> (Dubois 1908)	Unknown
<i>Cervus palaeomendjangang</i> (Dubois 1908)	Possibly junior synonym of <i>Cervus kendengensis</i> (Von Koenigswald 1933)
<i>Cervus problematicus</i> (von Koenigswald 1933)	Unknown
<i>Cervus</i> sp. (Martin 1888)	Unknown
<i>Cervus</i> (Dubois 1907)	Unknown
<i>Cervus (Rusa) sp.</i> (Dubois 1892)	Unknown
<i>Cervus (Rusa) sp.</i> (Von Koenigswald 1933)	Unknown
<i>Cervus</i> sp. (Stehlin 1925)	Unknown
<i>Cervus</i> sp. (Von Koenigswald 1933)	Unknown
<i>Cervus (Rusa) sp.</i> (Aziz & De Vos 1999)	Unknown
<i>Cervus</i> sp. (Stehlin & Umgrrove 1926)	Unknown

Table 3  
[Click here to download high resolution image](#)

Fossil species/ specimens	Subgenus	Included/ not included in linear morphometric analysis	Included/ not included in geometric morphometric analysis	Comments and tested hypotheses (in parenthesis)
<i>Axis lydekkeri</i>	<i>Hyelophus</i> ?	Included	Included	According to Meijaard & Groves (2004) this species belongs to the (sub-) genus <i>Hyelophus</i> . In addition this subgenus may not be closely related to <i>Axis</i> , and should possibly be considered a separate genus. Based on comparative measurements Zaim et al. (2003) argued that this species may be a senior synonym of <i>Cervus zwooni</i> . (Is <i>Axis lydekkeri</i> a synonym of <i>Axis zwooni</i> or perhaps other species? How is <i>Axis lydekkeri</i> related to the modern members of the genus <i>Axis</i> ?)
<i>Axis javanicus</i>	<i>Hyelophus</i> ? <i>Axis</i> ?	Included	not included	This species could be closely related or even synonymous to <i>Axis axis</i> (Meijaard & Groves 2004). (Is there reason to assume <i>A. javanicus</i> is a separate species?)
<i>Axis</i> sp. (Ngebung)	<i>Hyelophus</i> ? <i>Axis</i> ?	Included	not included	A small sample of cervid teeth were identified as <i>Axis</i> sp. by Bouteaux (2005) at Ngebung. Comparison of her measurements with a larger dataset was considered useful to potentially narrow down these identifications. (What species do the Ngebung <i>Axis</i> -deer belong to?)
<i>Cervus kendgensis</i>	<i>Rusa</i> ?	Included	Included	This species is similar in size and morphology to modern <i>Cervus (Rusa) timorensis</i> (Dubois 1908). (Is <i>C. kendgensis</i> synonymous with <i>C. timorensis</i> or any of the other larger species from the Pleistocene of Java?)
<i>Cervus zwooni</i>	<i>Rusa</i> ? <i>Axis</i> ? <i>Hyelophus</i> ?	Included	not included	According to Zaim (2003) <i>Cervus zwooni</i> is indistinguishable from <i>Axis lydekkeri</i> . Contrary to Von Koenigswald (1933), Zaim (2003) also states that there are no size differences between this species and <i>A. lydekkeri</i> . (Is <i>Cervus zwooni</i> a synonym for <i>Axis lydekkeri</i> ?)
<i>Cervus stehlini</i>	<i>Rusa</i> ?	Included	not included	Von Koenigswald (1933) recognized <i>Cervus stehlini</i> as a separate species, albeit very similar in size and morphology to <i>Cervus (Rusa) timorensis</i> . (Is this species related to- or perhaps even synonymous with- <i>Cervus (Rusa) timorensis</i> ?)
<i>Cervus timorensis</i> / <i>Cervus hippelaphus</i> (Pleistocene Java)	<i>Rusa</i>	Included	not included	Certain specimens were identified by von Koenigswald (1933, 1934) as <i>Cervus hippelaphus</i> , a junior synonym of <i>Cervus timorensis</i> , the extant Javan <i>Rusa</i> (Bouteaux 2005)
<i>Cervus</i> sp. (Pleistocene Sumatra)	<i>Rusa</i>	Included	Included	These fossils of the (sub-)genus <i>Rusa</i> have never been identified to species. Given the generally modern nature of the rest of the fauna (De Vos 1983) and the modern distribution of <i>Rusa</i> , it is likely they belong to <i>Cervus (Rusa) unicolor</i> . (To what fossil and/or modern deer species are the remains of <i>Cervus</i> sp. most closely related?)
<i>Cervus unicolor</i> (Pleistocene Laos, Vietnam)	<i>Rusa</i>	Included	not included	Measurements of this species from the Southeast Asian mainland were included by means of comparison.

Table 4  
[Click here to download high resolution image](#)

Modern Species	Subgenus	Number of specimens used in linear morphometric analysis	Number of specimens used in geometric morphometric analysis
Chital ( <i>Axis axis</i> )	<i>Axis</i>	68	14
Bawean deer ( <i>Axis kuhlii</i> )	<i>Hyelaphus</i>	2	2
Hog deer ( <i>Axis porcinus</i> )	<i>Hyelaphus</i>	23	8
Red deer ( <i>Cervus elaphus</i> )	<i>Cervus</i>	not included	14
Sambar ( <i>Cervus unicolor</i> )	<i>Rusa</i>	13	11
Javan rusa ( <i>Cervus timorensis</i> )	<i>Rusa</i>	15	8
Philippine spotted deer ( <i>Cervus alfredi</i> )	<i>Rusa</i>	4	3
Philippine deer ( <i>Cervus mariannus</i> )	<i>Rusa</i>	2	2
Eld's deer ( <i>Cervus eldii</i> )	<i>Rucervus</i>	not included	5
Barasingha ( <i>Cervus duvaucelii</i> )	<i>Rucervus</i>	not included	4
Père David's deer ( <i>Elaphurus davidianus</i> )	<i>Elaphurus</i>	not included	5
Fallow deer ( <i>Dama dama</i> )	<i>Dama</i>	not included	5
Fossil Species/specimens	Subgenus	Number of specimens used in linear morphometric analysis	Number of specimens used in geometric morphometric analysis
<i>Axis lydekkeri</i>	<i>Hyelaphus</i> ?	140	3
<i>Axis javanicus</i>	<i>Hyelaphus</i> ? <i>Axis</i> ?	3	not included
<i>Axis</i> sp. (Ngebung)	<i>Hyelaphus</i> ? <i>Axis</i> ?	5	not included
<i>Cervus kendengensis</i>	<i>Rusa</i> ?	28	15
<i>Cervus zwaani</i>	<i>Rusa</i> ? <i>Axis</i> ? <i>Hyelaphus</i> ?	7	not included
<i>Cervus stehlini</i>	<i>Rusa</i> ?	4	not included
<i>Cervus timorensis</i> (Pleistocene Java)	<i>Rusa</i>	10	not included
<i>Cervus</i> sp. (Pleistocene Sumatra)	<i>Rusa</i>	115	10
<i>Cervus unicolor</i> (Pleistocene Laos, Vietnam)	<i>Rusa</i>	59	not included

Table 5

[Click here to download high resolution image](#)

	C. kandoganus	A. kahlil	A. ans	A. porcinus	C. marianus	C. affinis	A. hydellari	A. sp. (Ngibung)	A. javanicus	C. sp. (Kali)	C. sp. (Sumatra)	C. unicolor (South mainland)
C. kandoganus	-	<0.001	<0.001	<0.001	0.044	0.006	<0.001	<0.001	0.079	0.002	<0.001	<0.001
A. kahlil	<0.001	-	0.007	0.354	0.094	0.437	0.467	0.721	0.306	0.091	<0.001	<0.001
A. ans	<0.001	0.007	-	<0.001	0.362	0.263	<0.001	0.805	0.330	0.001	<0.001	<0.001
A. porcinus	<0.001	0.354	<0.001	-	0.071	0.749	0.018	0.794	0.002	<0.001	<0.001	<0.001
C. marianus	0.044	0.094	0.362	0.071	-	0.938	0.505	0.751	0.255	0.163	0.044	<0.001
C. affinis	0.006	0.437	0.263	0.749	0.938	-	0.110	0.629	0.153	0.077	0.009	<0.001
A. hydellari	<0.001	0.467	<0.001	0.018	0.505	0.110	-	0.365	<0.001	<0.001	<0.001	<0.001
A. sp. (Ngibung)	<0.001	0.721	0.805	0.794	0.751	0.629	0.365	-	0.009	0.001	<0.001	<0.001
A. javanicus	0.079	0.306	0.330	0.002	0.255	0.153	<0.001	<0.001	-	0.138	0.043	0.002
C. kahlil	0.002	0.091	0.001	<0.001	0.163	0.077	<0.001	0.004	0.538	-	<0.001	<0.001
C. unicolor	<0.001	0.330	<0.001	0.042	0.309	0.269	<0.001	0.714	0.043	0.045	<0.001	<0.001
C. hypolephus (Hoad)	<0.001	<0.001	<0.001	<0.001	0.009	<0.001	<0.001	<0.001	0.044	0.000	<0.001	0.003
C. (Imoyus)	<0.001	0.005	<0.001	<0.001	0.044	0.019	<0.001	0.001	0.007	0.005	<0.001	<0.001
C. sp. (Sumatra)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-	<0.001
C. unicolor (North mainland)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-
C. unicolor	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.002	<0.001	<0.001	<0.001

Table 6  
[Click here to download high resolution image](#)

PC	Eigenvalue	% variance
1	0.00324146	60.064
2	0.0011354	21.039
3	0.000372339	6.8994
4	0.000286388	5.3068
5	0.000114931	2.1297
6	7.97E-05	1.4762
7	4.16E-05	0.77122
8	3.70E-05	0.68564
9	2.56E-05	0.47496
10	1.79E-05	0.33124
11	1.58E-05	0.29325
12	7.54E-06	0.13977
13	6.76E-06	0.12519
14	5.24E-06	0.097036
15	4.25E-06	0.078699
16	2.16E-06	0.039945
17	8,03E-07	0.014875
18	7.54E-07	0.013971
19	6.09E-07	0.011283
20	1.85E-07	0.0034326
21	9.67E-08	0.0017928
22	6.93E-08	0.0012844
23	5.89E-08	0.001091
24	4.86E-10	9.01E-06
25	3.47E-10	6.43E-06
26	1.09E-10	2.02E-06

Table 7

[Click here to download high resolution image](#)

	<i>A. axis</i>	<i>A. labili</i>	<i>A. lydekkeri</i>	<i>C. elongatus</i>	<i>C. leindingerensis</i>	<i>D. olsoni</i>	<i>C. divinatoris</i>	<i>E. davidsonis</i>	<i>C. elisi</i>	<i>A. percinus</i>	<i>C. offreni</i>	<i>C. timorensis</i>	<i>C. unicolor</i>	<i>C. manianus</i>	<i>C. sp. [Sumatra]</i>
<i>A. axis</i>	–	0.0095	0.0013	0.0001	0.0001	0.0003	0.0011	0.0001	0.0005	0.0001	0.0133	0.0001	0.0001	0.0083	0.0001
<i>A. labili</i>	0.0095	–	0.4902	0.0082	0.0071	0.0467	0.0725	0.0499	0.0462	0.3848	0.0983	0.0439	0.0094	0.3338	0.0157
<i>A. lydekkeri</i>	0.0013	0.4902	–	0.0008	0.0013	0.0189	0.0273	0.0364	0.0167	0.3334	0.0963	0.0123	0.0018	0.2061	0.0032
<i>C. elongatus</i>	0.0001	0.0082	0.0008	–	0.0001	0.0003	0.0029	0.0001	0.0284	0.0001	0.0038	0.0001	0.0005	0.0253	0.0001
<i>C. leindingerensis</i>	0.0001	0.0071	0.0013	0.0001	–	0.0001	0.0006	0.0004	0.0002	0.0001	0.0015	0.2524	0.0001	0.1580	0.0545
<i>D. olsoni</i>	0.0003	0.0467	0.0189	0.0003	0.0001	–	0.0080	0.0083	0.0081	0.0007	0.0174	0.0007	0.0003	0.0478	0.0004
<i>C. divinatoris</i>	0.0031	0.0725	0.0273	0.0029	0.0006	0.0080	–	0.0080	0.0172	0.0034	0.0276	0.0074	0.0060	0.0664	0.0140
<i>E. davidsonis</i>	0.0001	0.0490	0.0364	0.0001	0.0004	0.0083	0.0080	–	0.0078	0.0010	0.0172	0.0036	0.0204	0.0493	0.0004
<i>C. elisi</i>	0.0005	0.0462	0.0167	0.0284	0.0002	0.0001	0.0172	0.0078	–	0.0011	0.0190	0.0019	0.0024	0.0497	0.0019
<i>A. percinus</i>	0.0001	0.3848	0.3334	0.0001	0.0001	0.0007	0.0034	0.0019	0.0011	–	0.0066	0.0009	0.0001	0.1294	0.0005
<i>C. offreni</i>	0.0133	0.0983	0.0963	0.0038	0.0015	0.0174	0.0276	0.0172	0.0190	0.0066	–	0.0056	0.0044	0.1006	0.0038
<i>C. timorensis</i>	0.0001	0.0430	0.0123	0.0001	0.2524	0.0007	0.0074	0.0036	0.0019	0.0009	0.0056	–	0.0082	0.0796	0.5149
<i>C. unicolor</i>	0.0001	0.0094	0.0018	0.0005	0.0001	0.0003	0.0060	0.0204	0.0024	0.0001	0.0044	0.0082	–	0.4959	0.0019
<i>C. manianus</i>	0.0083	0.3338	0.2061	0.0253	0.1580	0.0478	0.0664	0.0493	0.0497	0.1294	0.1006	0.0796	0.4959	–	0.3152
<i>C. sp. [Sumatra]</i>	0.0001	0.0157	0.0032	0.0001	0.0545	0.0004	0.0140	0.0004	0.0019	0.0005	0.0038	0.5149	0.0019	0.3152	–

	<i>C. kendengensis</i>	<i>C. alfredi</i>	<i>C. timorensis</i>	<i>C. unicolor</i>	<i>C. mariannus</i>	<i>C. sp.</i>	Total
<i>C. kendengensis</i>	7 (46.6 %)	0	2 (13.3 %)	1 (6.6 %)	1 (6.6 %)	4 (26.6)	15
<i>C. alfredi</i>	0	2 (66.6 %)	0	1 (33.3 %)	0	0	3
<i>C. timorensis</i>	2 (25 %)	0	4 (50 %)	0	0	2 (25 %)	8
<i>C. unicolor</i>	2 (16.6 %)	1 (8.3 %)	0	8 (66.6 %)	1 (8.3 %)	0	12
<i>C. mariannus</i>	0	0	0	1 (50 %)	0	1 (50 %)	2
<i>C. sp.</i>	4 (40 %)	0	2 (20 %)	0	2 (20 %)	2 (20 %)	10
Total	15 (30 %)	3 (6 %)	8 (16 %)	11 (22 %)	4 (8 %)	9 (18 %)	50

	<i>C. kendengensis/ timorensis/ sp.</i>	<i>C. alfredi</i>	<i>C. unicolor</i>	<i>C. mariannus</i>	Total
<i>C. Kendengensis/ timorensis/ sp.</i>	29 (87.8 %)	0	1 (3 %)	3 (9 %)	33
<i>C. alfredi</i>	0	2 (66.6 %)	1 (33.3 %)	0	3
<i>C. unicolor</i>	2 (16.6 %)	1 (8.3 %)	8 (66.6 %)	1 (8.3 %)	12
<i>C. mariannus</i>	1 (50 %)	0	1 (50 %)	0	2
Total	32 (64 %)	3 (6 %)	11 (22 %)	4 (8 %)	50

Figure 1  
[Click here to download high resolution image](#)

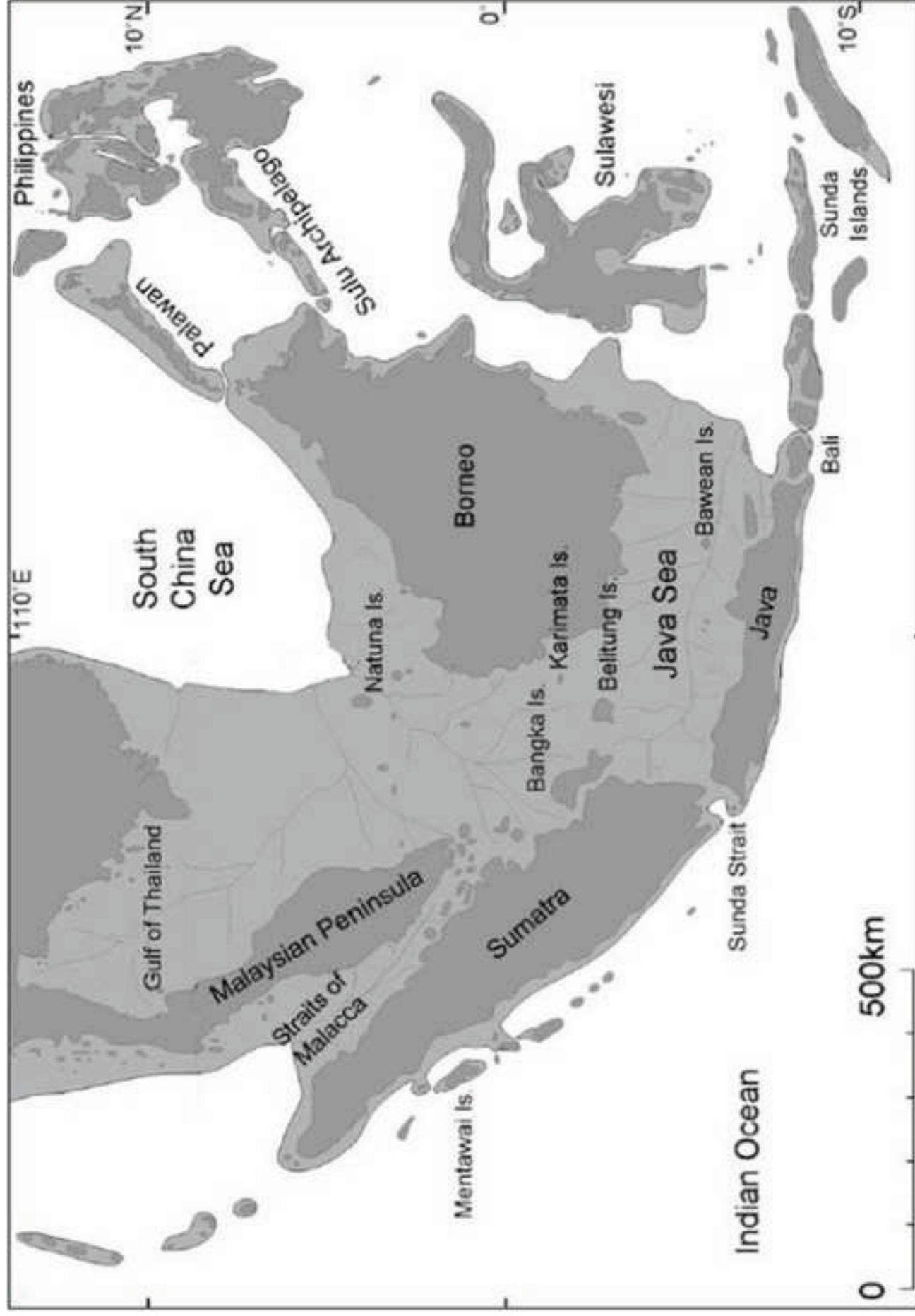
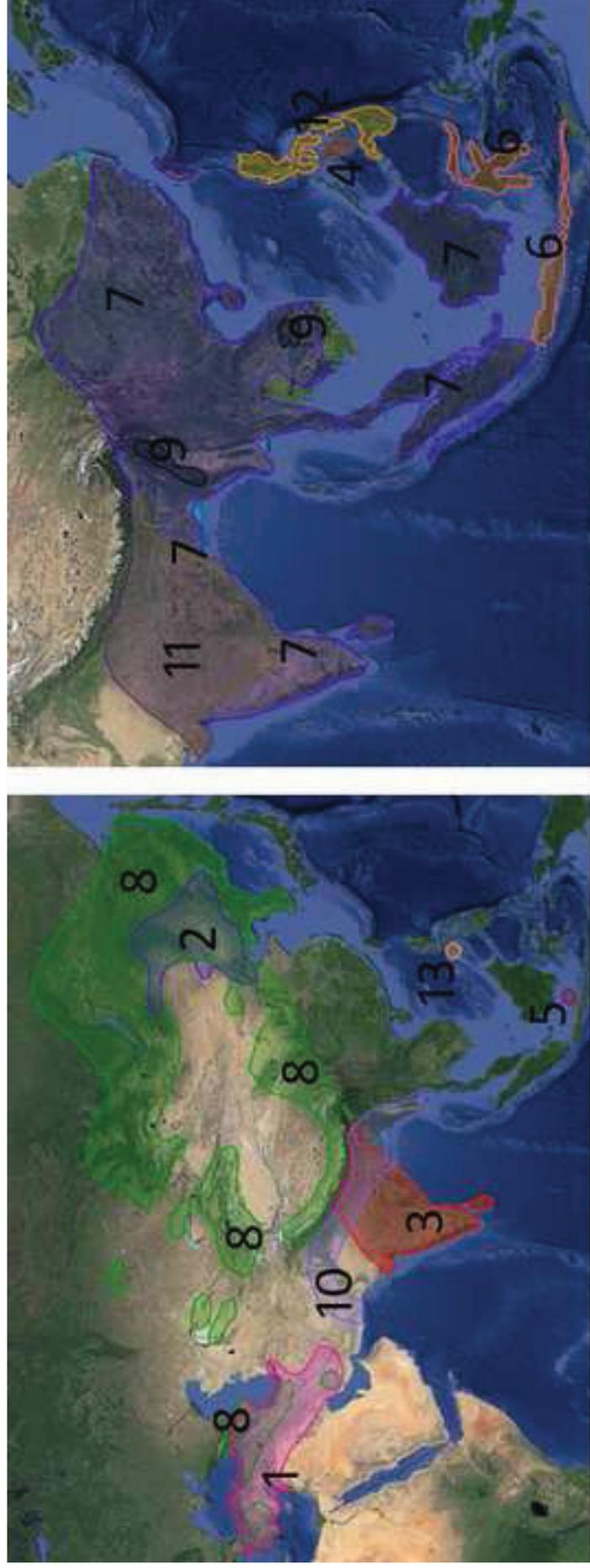


Figure 2  
[Click here to download high resolution image](#)



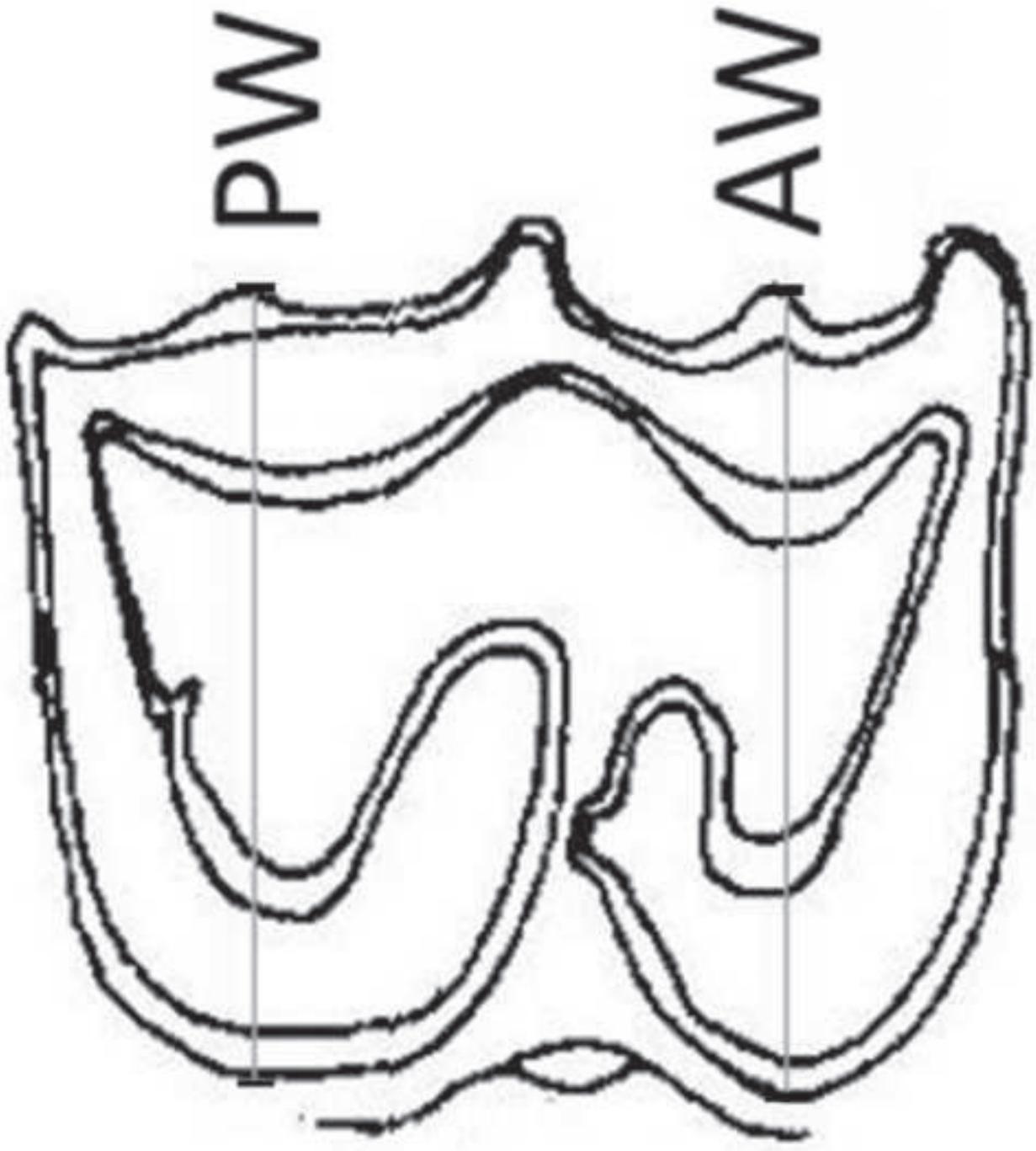


Figure 3  
[Click here to download high resolution image](#)

Figure 4  
[Click here to download high resolution image](#)

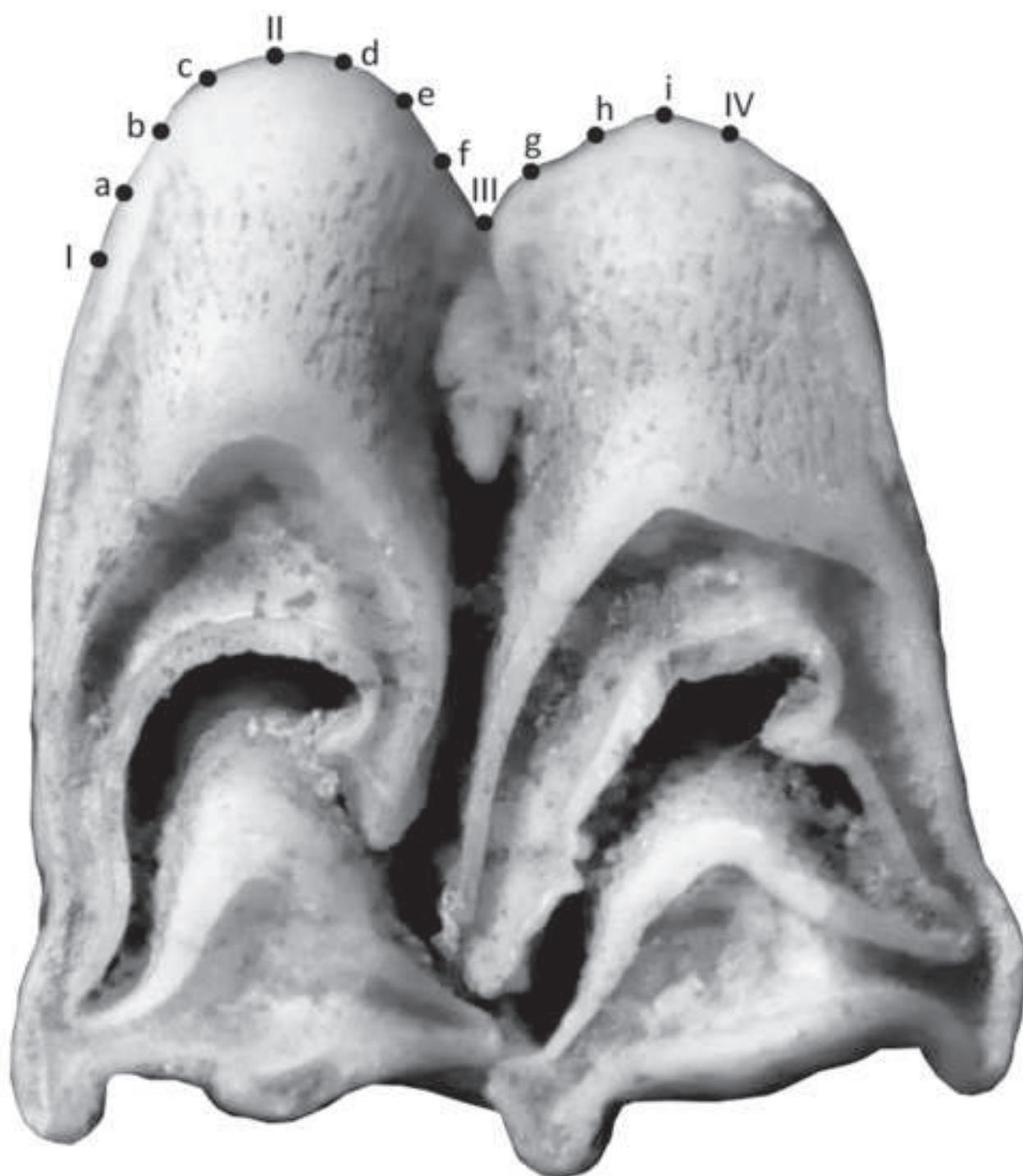


Figure 5  
Click here to download high resolution image

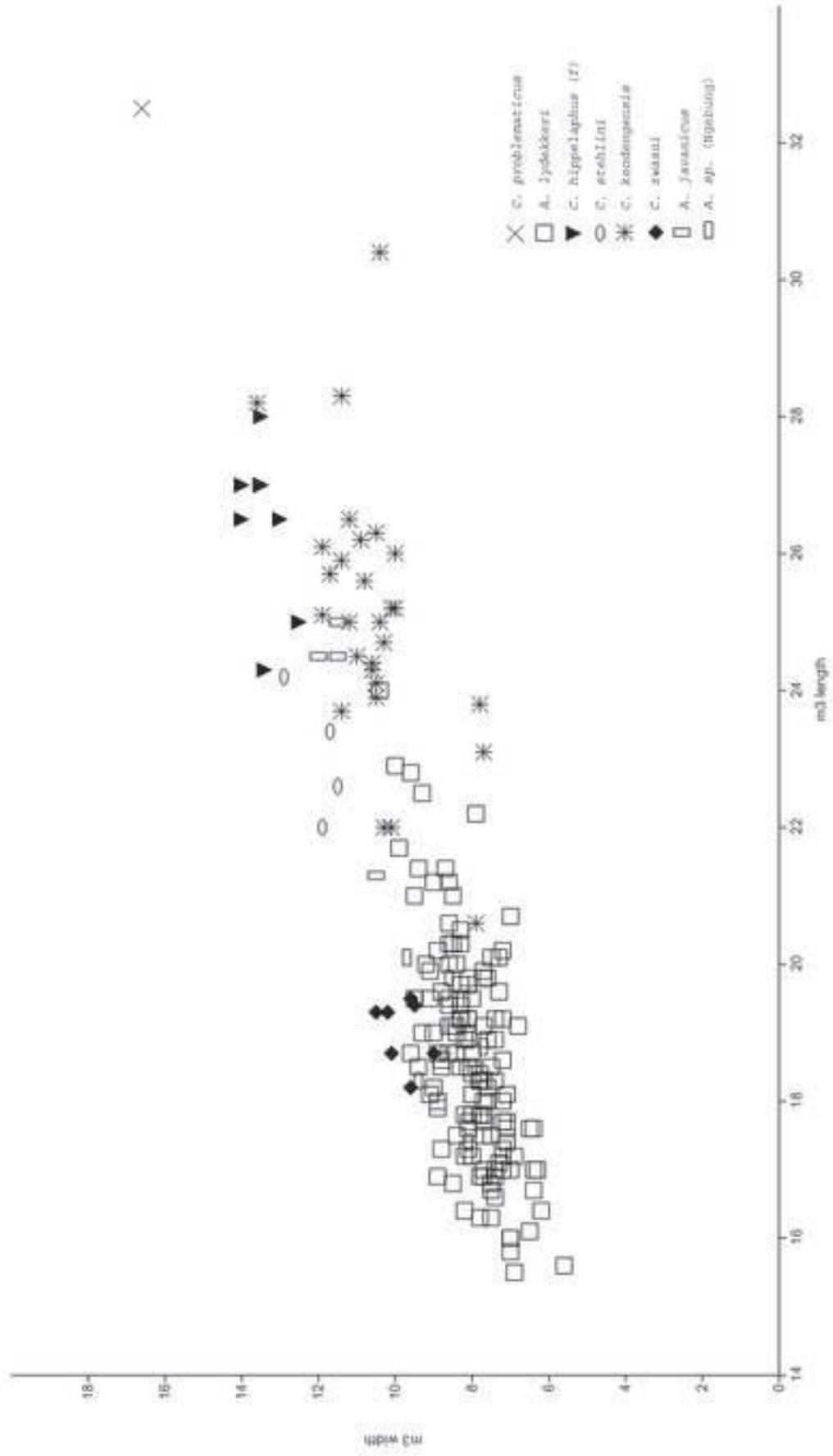


Figure 6  
Click here to download high resolution image

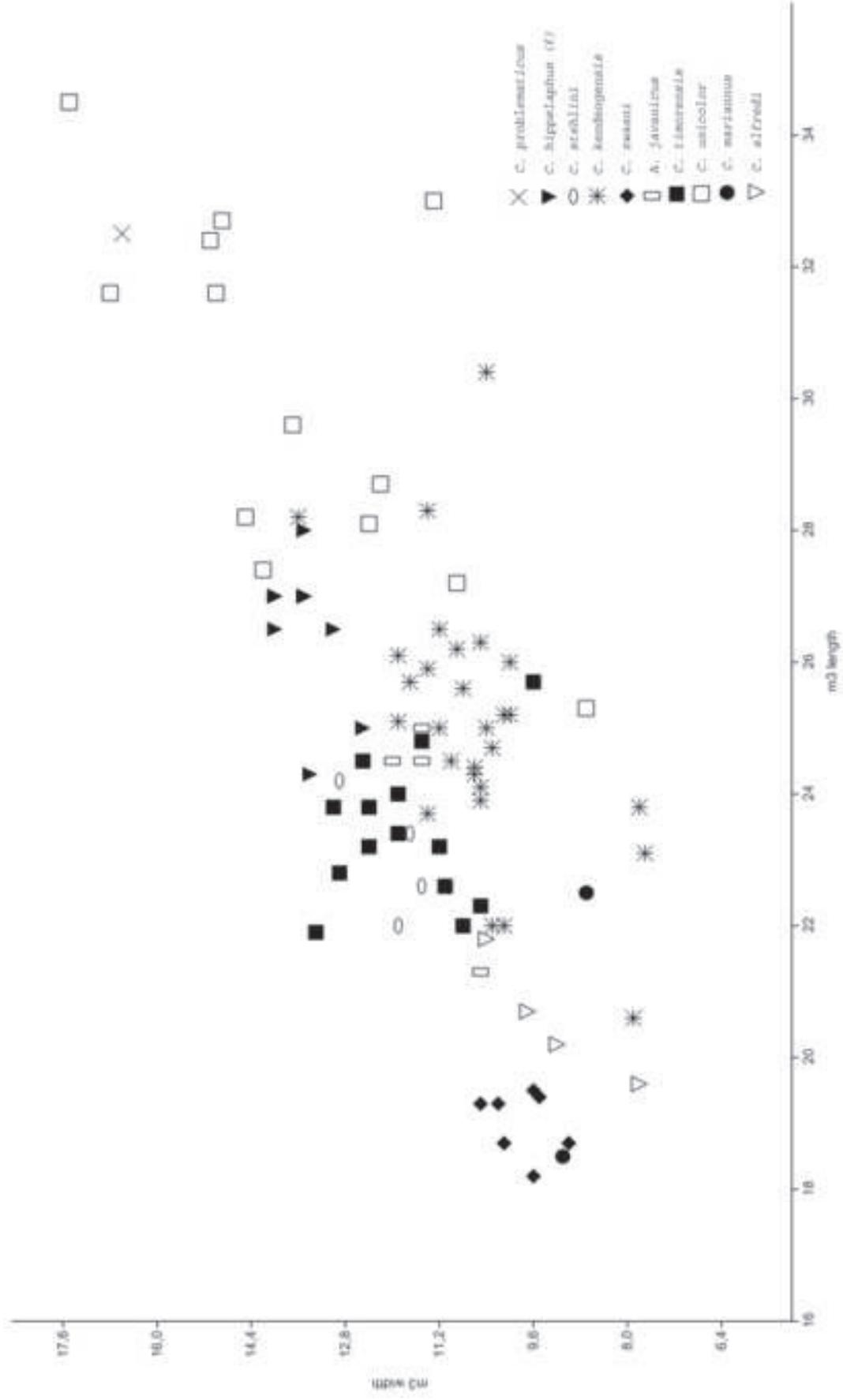


Figure 7  
Click here to download high resolution image

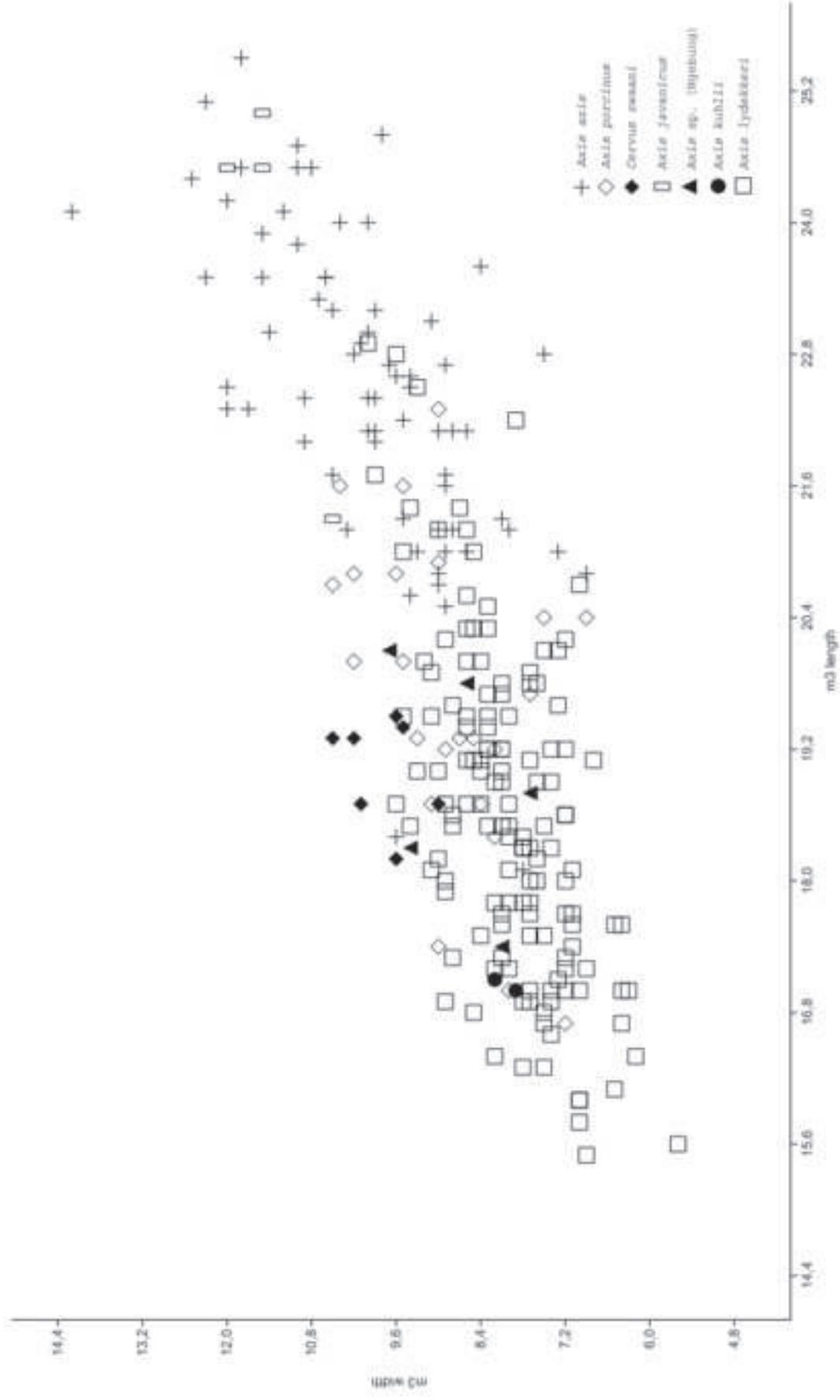


Figure 8  
[Click here to download high resolution image](#)

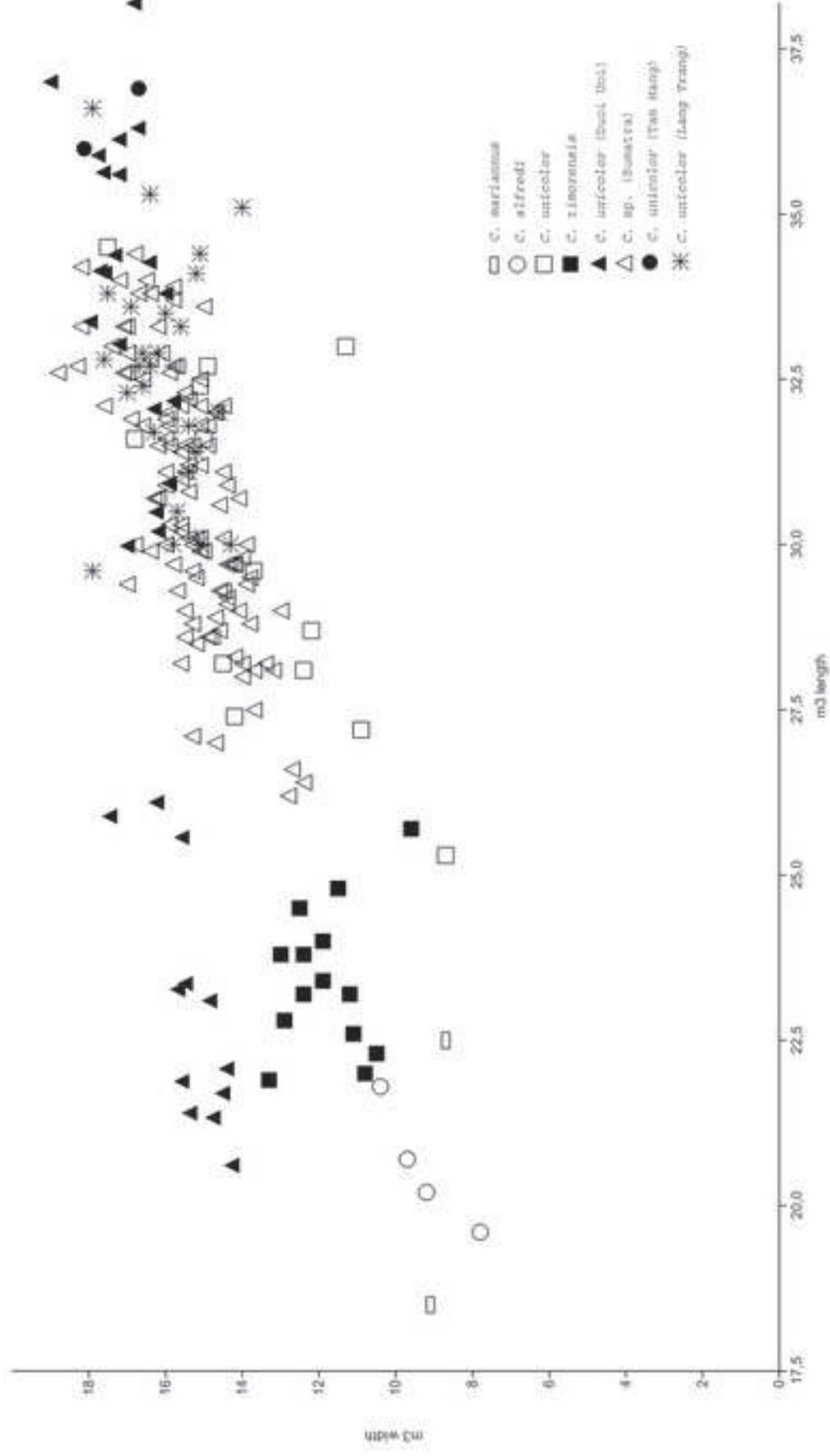


Figure 9  
Click here to download high resolution image

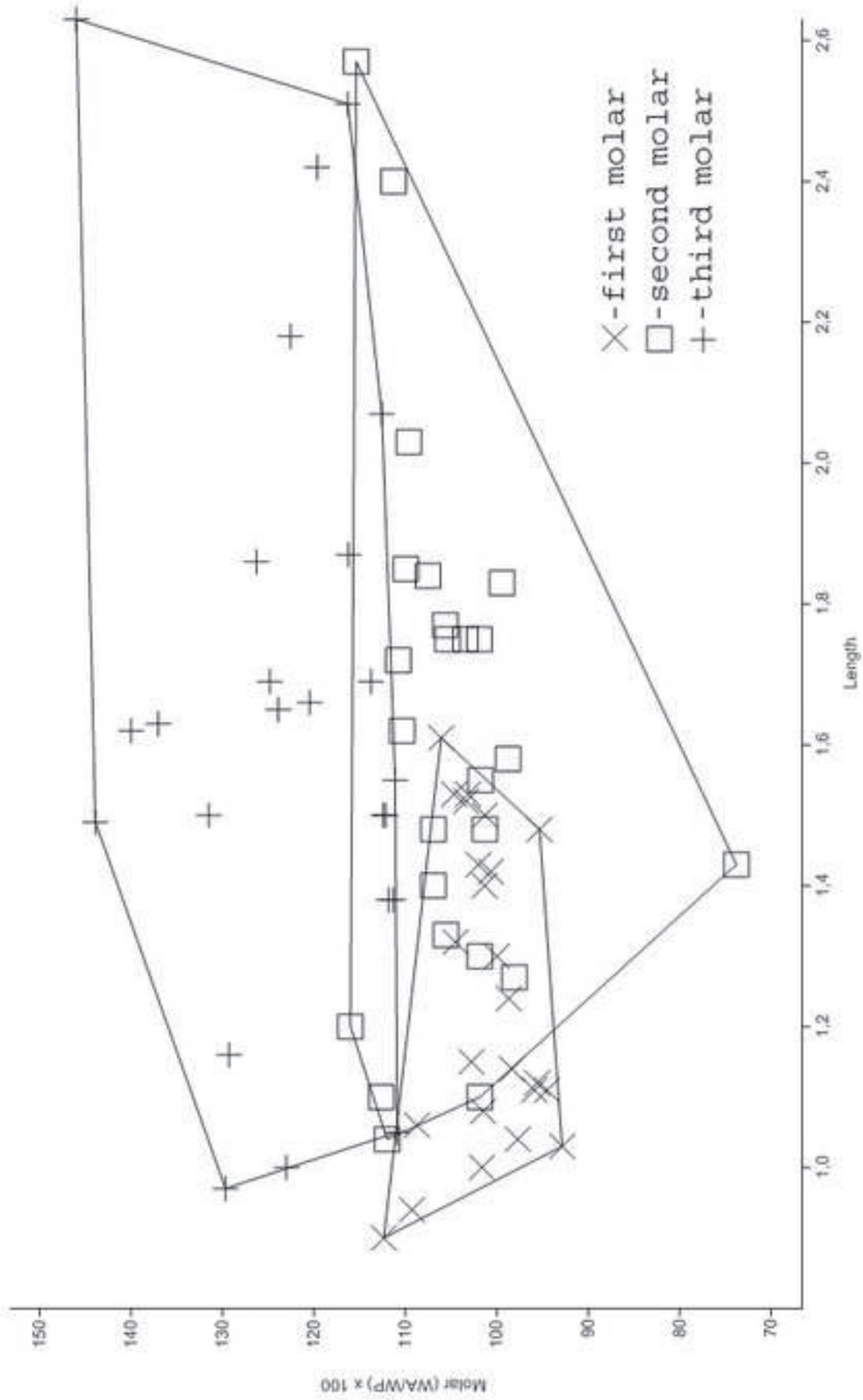


Figure 10  
[Click here to download high resolution image](#)

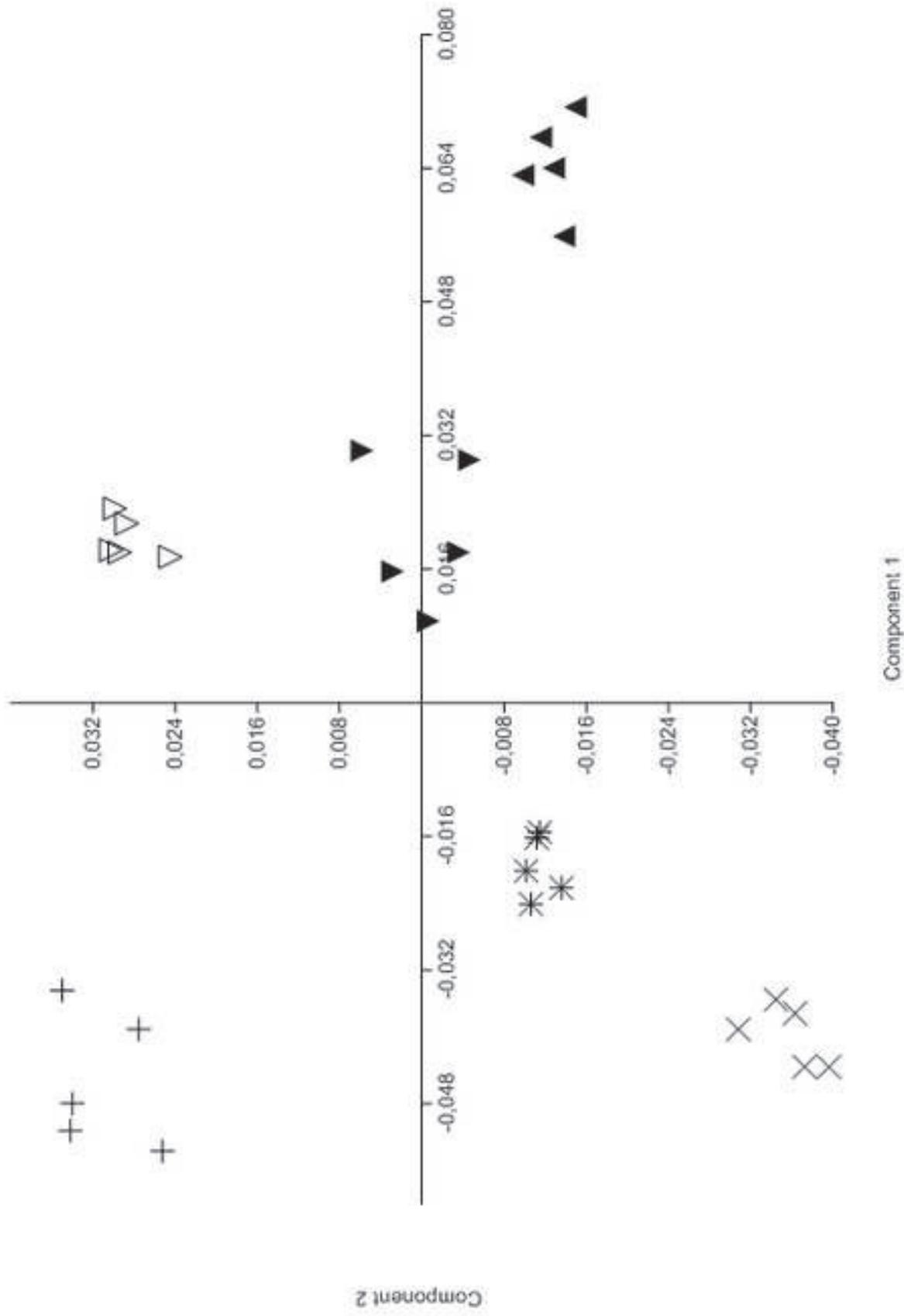


Figure 11  
Click here to download high resolution image

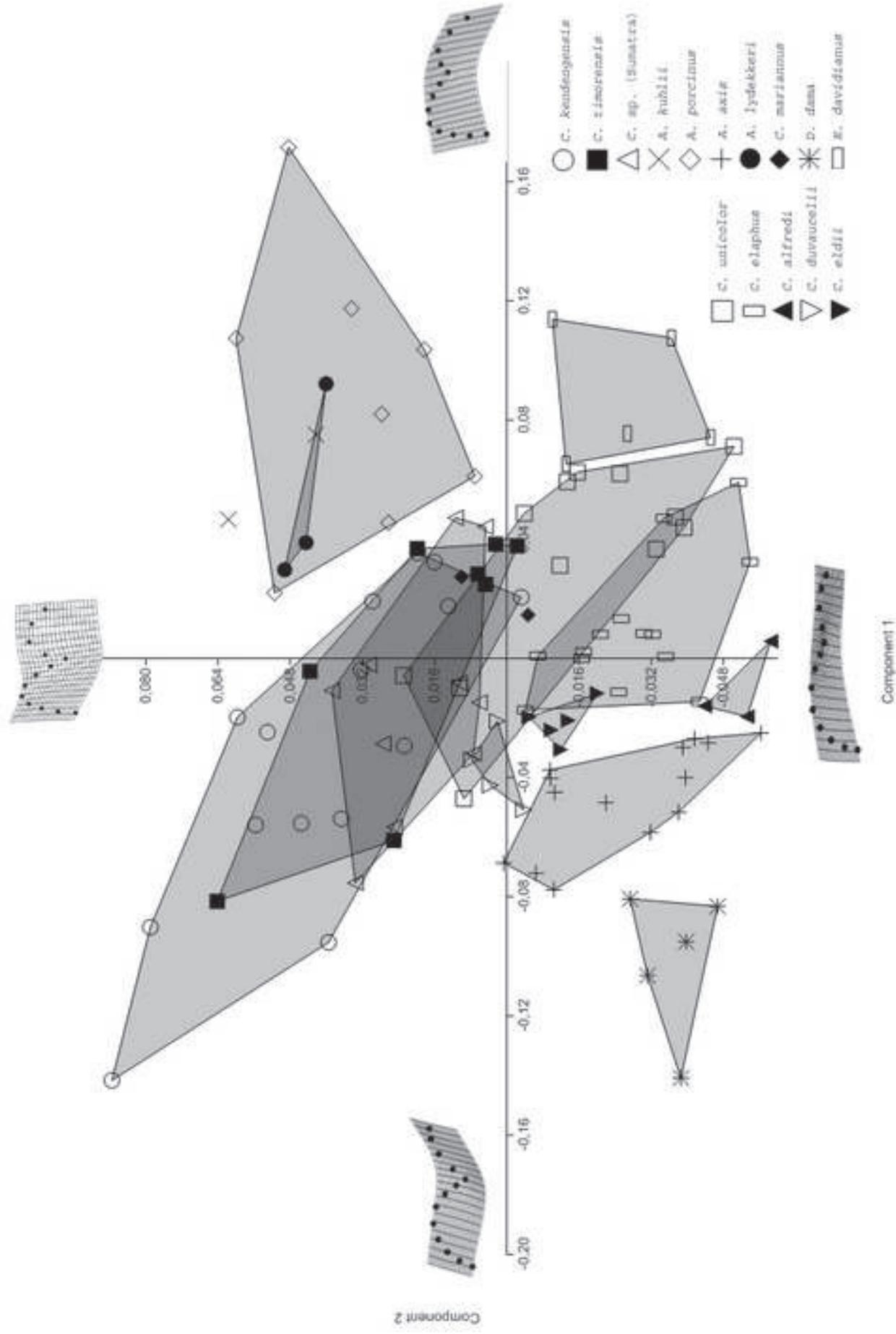
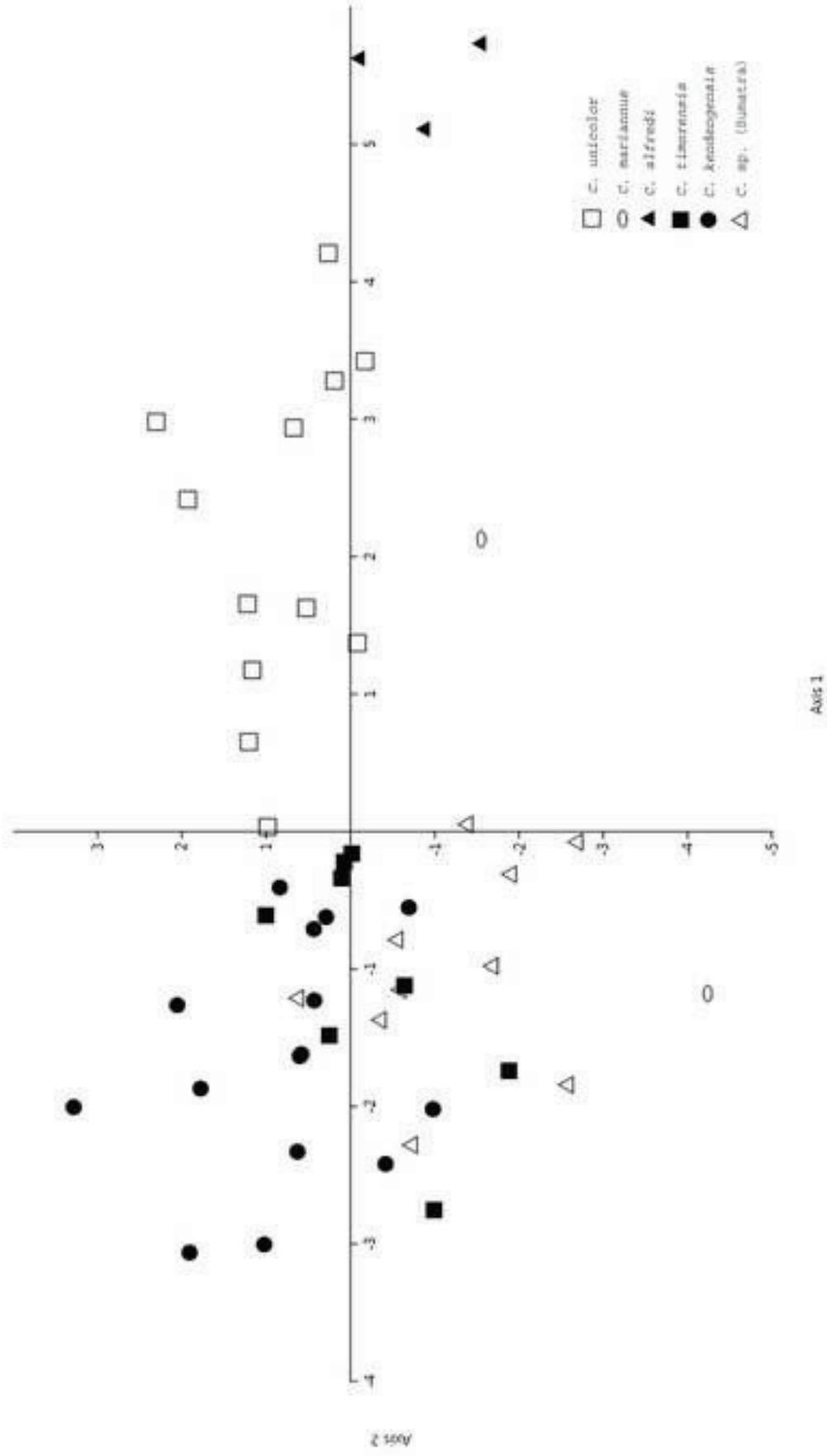


Figure 12  
[Click here to download high resolution image](#)



## Appendix A

[Click here to download Supplementary Data: Appendix A-measurements fossil deer molars.docx](#)

## Appendix B

[Click here to download Supplementary Data: Appendix B-measurements extant deer molars.docx](#)