

# Was *Cuon alpinus* a member of the Mammoth Steppe Fauna?

Comparative morphological and osteometrical study on recent and fossil Canidae hemimandibles.

Master thesis



Master thesis by

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Cover photo: fossil Canidae specimen NMR90, suspected to belong to *Cuon alpinus* (Dick Mol, pers. comm.).

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submitted in partial fulfillment of the requirements for the degree

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Also part of this thesis are appendices I – XIII (see supplement).





# Abstract

This master thesis focuses on thirteen Canidae hemimandibles fished from the bottom of the North Sea (Southern Bight) of which it remains to be established whether they belong to *Canis lupus lupus* (Eurasian wolf), *Canis lupus familiaris* (domestic dog) or *Cuon alpinus* (dhole). Of one hemimandible in particular (NMR90, a recently found posterior half of an extremely small jaw (with P<sub>4</sub> and M<sub>1</sub>) of estimated Late Pleistocene age) is suspected, due to its apparent small size and dental formula, that it most probably belongs to neither wolf nor dog (nor fox, which is considerably smaller), but to *Cuon alpinus* (Dick Mol pers. comm.). If this mandible were of *Cuon alpinus* origin, this would be the westernmost occurrence of *Cuon alpinus*, which is certainly a novelty for Dutch paleontology. The aim of this study was to identify the thirteen fossil North Sea specimens as wolf, dog or dhole and thereby verifying whether *Cuon alpinus* was a member of the carnivore guild of Northwestern Europe during the Late Pleistocene. The thirteen fossil North Sea specimens were identified by means of morphological and osteometrical comparison with comparative datasets of *Canis lupus lupus* (18 specimens), *Canis lupus familiaris* (42 specimens) and *Cuon alpinus* (27 specimens). All 100 Canidae specimens were measured for 21 parameters concerning hemimandibular and teeth dimensions. Additionally to all quantitative measurements, the fossil specimens were qualitatively compared to all three comparative (sub)species. Statistics (standard deviations) were applied to add a confidence interval of 97.7% to the conclusions that are based on the quantitative parameters. Keeping in mind that results may have been affected by: the representability of this particular comparative dataset for the *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* populations of Northwestern Europe during the Pleistocene (with respect to subspecies, locality, age and sex), differences between left and right hemimandibles, measuring errors, the normal distribution of parameters, values from literature and possible sexual dimorphism, this morphological and osteometrical study of the comparative Canidae material with the thirteen fossil North Sea specimens has allowed us to identify these fossil hemimandibles as belonging to the genus *Canis*. So far there is no evidence that *Cuon alpinus* was a member of the Mammoth Steppe Fauna.



# 1 Introduction

Recent *Cuon alpinus* ('dhole' in vernacular English) is a species of Canidae living in parts of Asia, including some islands such as Sumatra (Durbin et al., 2008). The present status of *Cuon alpinus* (the only still living species of the genus *Cuon*) is highly endangered, with probably no more than 2500 animals still living in the wild (Durbin et al., 2008). During the Late Pleistocene *Cuon alpinus* was more widespread and lived in Eurasia and North America (Durbin et al., 2008). It is however a rare fossil of which only few specimens have been described so far. Wolves and related Canidae (such as *Canis lupus lupus* and *Canis lupus familiaris*) are found more often. This also applies to fossils (mostly mandibles) from the bottom of the North Sea, although in younger material (Latest Pleistocene/Early Holocene) it remains to be established whether these mandibles belong to *Canis lupus lupus* (Eurasian wolf) or *Canis lupus familiaris* (domestic dog). Sometimes also very small mandibles are found in and around the North Sea, which are suspected to belong to the genus *Cuon* (Dick Mol pers. comm.).

This master thesis focuses on thirteen Canidae hemimandibles fished from the bottom of the North Sea, Southern Bight (from now on just called 'North Sea') and their morphological and osteometrical study (appendix I). It is expected that these hemimandibles belong to *Canis lupus lupus*, *Canis lupus familiaris* or *Cuon alpinus* (Jelle Reumer pers. comm.), but the identity of these fossils remains to be established. Of one hemimandible in particular (a recently found posterior half of an extremely small jaw (with P<sub>4</sub> and M<sub>1</sub>), appendix I, fig. I.13) is suspected that it most probably belongs to neither wolf nor dog (nor fox, which is considerably smaller), but to *Cuon alpinus* (Dick Mol pers. comm.). It is estimated that this mandible is from Late Pleistocene age (Dick Mol, pers. comm.). If this mandible were of *Cuon alpinus* origin, this would be the westernmost occurrence of *Cuon alpinus*, which is certainly a novelty for Dutch paleontology.

The aim of this master thesis is to identify the thirteen fossil hemimandibles from the North Sea by means of morphological and osteometrical comparison of these specimens to comparative datasets of the three (sub)species, which the thirteen specimens are suspected to be (*Canis lupus lupus*, *Canis lupus familiaris* and *Cuon alpinus*). Of particular interest hereby is fossil specimen NMR90 that is explicitly suspected to be *Cuon alpinus*:

*Was Cuon alpinus a member of the carnivore guild of Northwestern Europe during the Late Pleistocene?*

To answer this research question first will be verified whether the thirteen fossil North Sea specimens are indeed Canidae specimens and whether they indeed do not belong to the genus *Vulpes* (foxes). Subsequently the following hypotheses will be tested:

- The thirteen fossil hemimandibles from the North Sea are either *Canis lupus lupus*, *Canis lupus familiaris* or *Cuon alpinus*.
- Specimen NMR90 is a *Cuon alpinus* specimen.

The fossil specimens will be identified solely based on comparative morphological and osteometrical study of the fossils. Some paleontological background knowledge is useful to the reader, although the most important (osteometrical) definitions and terminology are given in the appendices.



## 2 Material & Methods

In this study 100 Canidae specimens were morphologically and osteometrically analyzed (appendices II and XIII). In the 'Material' section the thirteen fossil specimens from the North Sea and the comparative dataset are presented to the reader. The most prominent features of each fossil North Sea specimen will be discussed and a general description of the comparative dataset (that includes *Canis lupus lupus*, *Canis lupus familiaris* and *Cuon alpinus* specimens) is given. In the 'Methods' section 21 morphological and osteometrical parameters that were taken and all (osteometrical and statistical) methods that were used in this study to analyze the hemimandibles will be explained.

### 2.1 Material

The assemblage of 100 Canidae specimens that was used in this study consist of the 13 fossil North Sea specimens of which the identity must be determined and 87 comparative fossil and recent *Cuon alpinus*, *Canis lupus lupus* and *Canis lupus familiaris* specimens (see appendix II for a list of all Canidae material and 3.1 for the Canidae taxonomy that is used in this thesis). Almost all specimens of the reference material come from the Canidae collection deposited in the Netherlands Centre for Biodiversity NCB Naturalis (Leiden, The Netherlands). Three comparative *C. l. lupus* specimens (NMR86, NMR87 and NMR88) and two fossil North Sea specimens (NMR89 and NMR90) come from the Natuurhistorisch Museum Rotterdam, NMR (The Netherlands). The remaining 11 fossil North Sea specimens come from the private collection of Mr. Kommer Tanis.

Additionally to the values of all parameters that are taken on each specimen the following information (if available) was recorded for all material: scientific name, locality (where the specimen was acquired), sex, age (of the fossil), date on which the specimen was collected, by whom the specimen was collected (legit), by whom the specimen was donated to the museum, the specimen registration number, the category number and other information when present (such as details on the site where fossil specimens were found) (appendices II and XIII). Most of this information is not relevant for this study and was only recorded to easily retrieve a specific specimen from the huge collection of NCB Naturalis. The registration numbers whether or not in combination with the category number are unique for each specimen and will be used to refer to a specific specimen. The remaining relevant information (scientific name, locality, sex and age) is discussed below for all material and can be found in appendix II.

#### 2.1.1 Fossil material from the North Sea

The only information that is available for all 13 fossil North Sea specimens is that they belong to the Canidae and were found in the North Sea (appendix II). No further information (such as age and sex) is known. Each specimen is briefly presented below. For all terminology used to describe the hemimandibles see appendix III and fig. IV.1 and IV.2.

##### 1. Specimen 534

This fossil specimen is a posterior part of the mandibular body (including ramus) of a very large left hemimandible (appendix I). The entire part of the hemimandible anterior of the second (distal) alveole of the  $M_1$  is missing. The ascending ramus is still present, but severely eroded: the apex of the coronoid process, the condyle and the angular process are missing. Specimen 534 still possess an  $M_2$  and a small and rounded, but clear alveole of the slightly eroded  $M_3$  (plate 4.1). The most posterior part of the second alveole of the  $M_1$  is also visible.

##### 2. Specimen 535

Fossil North Sea specimen 535 is a posterior part of the mandibular body of a quite large right hemimandible (appendix I). The entire part of the hemimandible anterior of the  $M_1$  is missing. Most part of the ramus is also eroded: the entire coronoid process and condyle are missing and the angular process is severely eroded. This specimen still possesses an  $M_1$  and  $M_2$  that are hardly eroded and in which cusps are present in their original state (plate 4.1). The hemimandible also possesses a well-defined, small and rounded alveole of its  $M_3$ .

##### 3. Specimen 667

Specimen 667 is an almost complete, average-sized right hemimandible (appendix I). The apex of the coronoid process, the condyle and the angular process are slightly eroded and the most anterior part of the hemimandible, at the position of the canine, is missing. All teeth (except the incisors, canine and third molar) are still present, but the tops of the cusps are eroded (plate 4.1). At the place where the  $M_3$  should be

located a well-defined, small and rounded alveole is present and part of the alveole of the canine can still be seen. The alveole of the P<sub>1</sub> is only filled with the root (cervical third) of this tooth: the middle and apical third of the P<sub>1</sub> are eroded.

#### **4. Specimen 1683**

This fossil specimen is a substantial part of the mandibular body of a very large right hemimandible (appendix I). A large part of the ramus, including the condyle and angular process, and the most anterior part of the hemimandible, at the position of the canine, are missing. All teeth (except the incisors and canine) are still present, but the tops of the cusps are slightly eroded (plate 4.1). Part of the alveole of the canine can still be seen. The P<sub>1</sub> is broken off at the middle third of the tooth and the crown (apical third) is missing.

#### **5. Specimen 2103**

Fossil North Sea specimen 2103 is an almost complete, average-sized left hemimandible (appendix I). The ramus is entirely intact and only the most posterior part of the angular process is slightly eroded. A small anterior part of the hemimandible, containing I<sub>1</sub> and I<sub>2</sub>, is missing. The P<sub>2-4</sub> and M<sub>1</sub> are still present in original state (cusps are not eroded). At the place where the M<sub>3</sub> and P<sub>1</sub> should be located a well-defined, small and rounded alveole is present. The alveoles of the M<sub>2</sub>, I<sub>3</sub> and canine can also still be seen (plate 4.1).

#### **6. Specimen 2104**

Specimen 2104 is very similar in appearance to specimen 2103: it is a complete, average-sized left hemimandible (appendix I). The ramus is entirely intact and only the most posterior part of the angular process and a lingual part of the condyle are slightly eroded. No parts are eroded from the anterior part of the hemimandible; the mandible of this animal was broken into two exactly at the mandibular symphyse. The P<sub>2</sub> - M<sub>2</sub> are still present and only the cusps of the M<sub>1</sub> are eroded. At the place where the M<sub>3</sub> and P<sub>1</sub> should be located a well-defined, small and rounded alveole is present. The alveoles of the canine and all three incisors can also still be seen (plate 4.1).

#### **7. Specimen 2196**

This fossil specimen is a substantial part of the mandibular body of a very large left hemimandible (appendix I). Almost the entire ramus including the condyle and angular process, and the most anterior part of the hemimandible, anterior of the canine, are missing. All teeth (except the M<sub>3</sub>) are still present and the cusps of the P<sub>2</sub> and M<sub>1</sub> are slightly eroded (plate 4.1). All other teeth are in the original state. A small, round alveole is present at the position where the single-rooted M<sub>3</sub> was originally present. The entire alveole of the canine is also visible.

#### **8. Specimen 2329**

Specimen 2329 is an almost complete, very large left hemimandible (appendix I). The ramus is still entirely intact and only the buccal part of the condyle and the most posterior part of the angular process are eroded. The most anterior part of the hemimandible, anterior of the canine, is missing. The P<sub>2</sub> - M<sub>1</sub> are still present but the tops of the cusps of these teeth are slightly eroded. At the place where the M<sub>3</sub> and P<sub>1</sub> should be located a well-defined, small and rounded alveole is present. The alveoles of the canine and M<sub>2</sub> can also still be seen and a small part of the second (distal) root of M<sub>2</sub> is still present (plate 4.1).

#### **9. Specimen 2620**

This fossil North Sea specimen is a highly eroded part of the mandibular body of a very large right hemimandible (appendix I). The mandible of this animal was broken into two at the mandibular symphyse and of the most anterior part of the hemimandible only the part containing the I<sub>1</sub> is missing. The lower part of the mandibular body is broken off from below the P<sub>4</sub> towards the most posterior part of this specimen and the entire ramus is missing. Almost all teeth (except the I<sub>1</sub>, P<sub>1</sub> and M<sub>3</sub>) are present, but are severely eroded (plate 4.1). A P<sub>1</sub> and corresponding alveole are entirely missing: a diastema is situated between the canine and P<sub>2</sub>. A small, round alveole is present at the position where the single-rooted M<sub>3</sub> was originally present.

#### **10. Specimen 3219**

This fossil specimen is a part of the mandibular body of an average-sized left hemimandible (appendix I). The entire ramus and the most anterior part of the hemimandible including the I<sub>1</sub> are missing. The P<sub>2</sub> - M<sub>1</sub> are still present and the tops of the cusps of these teeth are only slightly eroded. The alveoles of the P<sub>1</sub> and I<sub>3</sub> are filled with the root (cervical third) of this tooth: the middle and apical third of these teeth are eroded. At the place where the I<sub>2</sub>, canine and M<sub>2</sub> originally were present, clear alveoles can be seen. A P<sub>1</sub> and corresponding alveole are entirely missing: a diastema is situated between the canine and P<sub>2</sub> (plate 4.1).

### 11. Specimen 3293

Specimen 3293 is a part of the mandibular body of a quite large left hemimandible (appendix I). The entire ramus and the most anterior part of the hemimandible, at the position of the canine, are missing. All teeth (except the incisors and canine) are still present and the cusps are hardly eroded (plate 4.1). The mesial part of the P<sub>2</sub> and P<sub>3</sub> (the middle and apical thirds of the teeth, above the mesial root) are entirely eroded.

### 12. Specimen NMR999100006889 (NMR89)

This specimen (from now on abbreviated to NMR89) is an almost complete left hemimandible (appendix I). The uppermost part of the ramus (including the apex and posterior angle of the coronoid process) is missing and the condyle and angular process are severely eroded. The most anterior part of the hemimandible, anterior of the P<sub>2</sub>, is missing, but part of the alveole of the second (distal) root of P<sub>1</sub> can still be seen. NMR89 does not possess teeth anymore, but the alveoles of the P<sub>2</sub>-M<sub>3</sub> can clearly be seen (plate 4.1). This specimen was found at the Southern Bight (North Sea).

### 13. Specimen NMR999100006890 (NMR90)

Specimen NMR90 is a posterior part of the mandibular body (including ramus) of an average-sized right hemimandible (appendix I). The apex of the coronoid process, the condyle and the angular process are eroded and the anterior part of the hemimandible, anterior of the P<sub>4</sub>, is missing. The entire lower part of the mandibular body is eroded over the length of the entire specimen. NMR90 still possesses a P<sub>4</sub> and M<sub>1</sub> of which the cusps are quite eroded. An alveole is situated at the position where originally an M<sub>2</sub> was present. An M<sub>3</sub> and corresponding alveole are entirely missing (plate 4.1). This specimen was also found at the Southern Bight (North Sea). NMR90 is of specific interest for this study, because Dick Mol suspects that this specimen most probably belongs to *Cuon alpinus*. It is estimated that this mandible is from Late Pleistocene age (Dick Mol, pers. comm.).

## 2.1.2 Comparative material

The comparative dataset consists of: 27 *Cuon alpinus* specimens, 42 *C. l. familiaris* specimens and 18 *C. l. lupus* specimens (87 specimens in total) (appendix II). This includes all *Cuon alpinus* and *C. l. lupus* material that is available in NCB Naturalis and a selection of the *C. l. familiaris* material present there. In this selection as many as possible localities and dog breeds were included to make the comparative *C. l. familiaris* dataset as representative as possible for the entire *C. l. familiaris* subspecies.

The comparative *Cuon alpinus* dataset consists of the subspecies *Cuon a. dukhunensis*, SYKES, 1831, *Cuon a. javanicus* DESMAREST, 1820, *Cuon a. rutilans*, MÜLLER, 1839 and some *Cuon alpinus* PALLAS, 1811 specimens for which no subspecies was defined (appendix II). Nowadays all subspecies of *Cuon alpinus* are considered as one species: *Cuon alpinus* PALLAS, 1811 (Anderson and Jones, 1984). Twenty-five *Cuon alpinus* specimens come from Java, one comes from India (specimen 20551) and one from Siberia (specimen Cuon-a-sib). In this dataset only recent *Cuon alpinus* specimens are included, because no fossil *Cuon alpinus* specimen were present in the collection at NCB Naturalis. From this point on, this entire *Cuon alpinus* dataset will be treated as one group; no distinction will be made between the different subspecies or localities.

The comparative *C. l. lupus* dataset consists of 17 *Canis. l. lupus* LINNAEUS, 1758 specimens from localities throughout Europe and one *Canis. l. nubilus* SAY, 1823 specimen from Tennessee (appendix II). Fourteen specimens are recent and four are fossil. Only the age of fossil specimen 445834 is known: Weichselien. In the rest of this study this comparative *C. l. lupus* dataset will be treated as one group; no distinction will be made between different subspecies, localities or recent and fossil material.

The comparative *C. l. familiaris* dataset entirely consists of *Canis. l. familiaris* LINNAEUS, 1758 specimens. For seven specimens also the dog breed is known (appendix II). This dataset includes 20 recent *C. l. familiaris* specimens and 22 fossil *C. l. familiaris* specimens of Weichselien age. This comparative dataset can also be divided into two groups based on a geographical variable: the *C. l. familiaris* dataset consists of 13 specimens from Suriname and 29 specimens from several localities throughout the Netherlands. The specimens from Suriname are all recent material and the specimens from the Netherlands are mainly fossil. On the contrary to *Cuon alpinus* and *C. l. lupus*, where only a few specimens are present for each variable, the sample sizes of the two *C. l. familiaris* groups (the recent specimens from Suriname and the fossil specimens from the Netherlands) are sufficiently large to analyze the groups separately. In the rest of this study the entire comparative *C. l. familiaris* dataset will be used to compare the 13 fossil North Sea specimens to, but the two *C. l. familiaris* groups will also be analyzed separately to see if there are any important differences between these two groups due to the temporal or geographical variable.

For all three comparative (sub)species the sex is not known for most specimens. For the specimens for which the sex is known the distribution male-female is approximately fifty-fifty. However, the amount of specimens for which sex is known is too small to base conclusions on. Possible differences between specimens based on sex(ual dimorphism) will not be discussed. A remarkable observation in the comparative material is that all recent material consists of entire skulls (mandibles and maxillas) and that all fossil material consists of only hemimandibles.



## 2.2 Methods

### 2.2.1 Morphological and osteometrical parameters

As many as possible morphological and osteometrical parameters that can be measured on hemimandibles and are known or suspected to be indicative of *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* (thus for which these three (sub)species have distinct and different values) were acquired from literature. This resulted in a list of 21 parameters that are classified into four groups according to the feature of the mandible (mandible length, mandible (width, height and ratios), ramus or teeth) of which each parameter is indicative (box 2.1). Since it was never explained in the literature what the exact definitions of the parameters are or how they were taken, the measuring methods of all 21 parameters were (re)defined for this study and a full description of each parameter is given in appendix IV.

Box 2.1: List of all 21 parameters	
<p><b>Mandible length</b></p> <ol style="list-style-type: none"> <li>1. Length of the mandible (<i>a-b</i> and <i>c-b</i>).</li> <li>2. Alveolar length of a specified tooth row (P<sub>1</sub>-M<sub>2</sub>, P<sub>4</sub>-M<sub>1</sub>-M<sub>2</sub> and M<sub>1</sub>-M<sub>2</sub>).</li> <li>3. Diastema length between two specified teeth of the mandible (C-P<sub>1</sub>, P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub>).</li> <li>4. Mental foramina (middle and posterior).</li> <li>5. Incisors.</li> </ol>	<p><b>Mandible (width, height and ratios)</b></p> <ol style="list-style-type: none"> <li>6. Width of the mandible (<i>i-i'</i> and <i>k-k'</i>).</li> <li>7. Distance <i>h-h'</i> under the mandibular teeth (P<sub>1</sub>, P<sub>2</sub>, P<sub>3</sub>, P<sub>4</sub>, M<sub>1</sub>, M<sub>2</sub>).</li> <li>8. Length, width and height ratios of the mandible.</li> </ol>
<p><b>Ramus</b></p> <ol style="list-style-type: none"> <li>9. Distance <i>a-d</i> of the mandible.</li> <li>10. Distance <i>e-e'</i> of the mandible.</li> <li>11. Coronoid angle (<math>\nu</math>).</li> <li>12. Aboral border of the ramus.</li> <li>13. Anterior border of the coronoid process.</li> <li>14. Angular process.</li> <li>15. Relation between the angular process and the mandibular condyle (line <i>k</i>).</li> </ol>	<p><b>Teeth</b></p> <ol style="list-style-type: none"> <li>16. Dental formula (presence of M<sub>3</sub>).</li> <li>17. Height of the crown of a specified tooth (P<sub>4</sub> and M<sub>1</sub>).</li> <li>18. Length of a specified tooth (M<sub>1</sub> and M<sub>2</sub>).</li> <li>19. Breadth of a specified tooth (M<sub>1</sub> and M<sub>2</sub>).</li> <li>20. Cusps of the premolars.</li> <li>21. Cusps of the molars.</li> </ol>

### 2.2.2 Measuring methods

#### Photographs

All photos included in this report and the appendices were taken with a Fujifilm FinePix E900 Digital Camera (9.00 megapixel resolution, Fujinon 4.00x optical zoom lens F2.8-F5.6, focal length: 7.2-28.8mm) by the author and André Slupik (of the Natuurhistorisch Museum Rotterdam, NMR).

#### Measuring equipment

The measuring equipment that was used to measure all 21 parameters on the 100 Canidae specimens consisted of:

- An analogue caliper. Accuracy of 1 mm.
- An electronic digital caliper. Length: 1-150 mm, accuracy: 0.02 mm.
- Set square. Accuracy of 1 (arc)degree.

All quantitative parameters were measured with either of the two calipers in mm. The coronoid angle was measured with the set square in degrees. Two different calipers were used, because the range of the digital caliper is limited: some *C. l. lupus* and *C. l. familiaris* specimens had values for the parameter 'Length of the mandible (*a-b* and *c-b*)' that were larger than the maximum length that the digital caliper can measure (150 mm). Since the accuracy of the analogue caliper is lower than that of the digital caliper the use of this caliper was restricted to only those specimens that could not be measured with the digital caliper (which includes a limited number of *C. l. lupus* and *C. l. familiaris* specimens only for the parameter 'Length of the mandible *a-b* and *c-b*' (in appendix XIII the specimens that were measured with the analogue caliper are indicated in italic). The two calipers and the set square were read off according to their accuracy: the analogue caliper with zero digits behind the decimal point, the digital caliper with two digits behind the decimal point (both in mm) and the set square with zero digits behind the decimal point (in degrees). For all outcomes of calculations (2.2.3 and 2.2.4) a maximum of two significant digits behind the decimal point is used. Note that in English decimal points are used differently than in Dutch (1.000 = 1 in English, while 1.000 = 1000 in Dutch and 1,000 = 1000 in English, while 1,000 = 1 in Dutch). In all text of this thesis the decimal points are

used as in English, but in all tables and graphs the decimal points are used as in Dutch, since tables and graphs were made with a Dutch Excel program.

#### *Left hemimandibles*

All parameters were measured on the left hemimandible of all 100 Canidae specimens, except when only a right hemimandible was present or when the left hemimandible was eroded for a certain parameter. In that case the antimere was measured instead. Initially parameters were measured on both the right and left hemimandible, but soon it became evident that the differences between the two hemimandibles are absent or very small (especially with the digital caliper) and in the same order of size as the measuring error (2.2.3). Due to the similar order of size, one cannot know whether the difference that is measured is caused by a significant difference between the two hemimandibles or by the measuring error. Moreover, one could question whether it is really relevant to measure differences between right and left hemimandibles for this particular study. The values of parameters taken on the left hemimandible are representative for that specimen. The fact that left and not right hemimandibles were measured is arbitrarily.

#### *Estimated values*

Most of the 13 fossil North Sea specimens are partly eroded and not all 21 parameters could be measured on every specimen (appendix I). In some of these cases it was still possible to make a reasonable estimate of the value for that parameter based on the remaining part of the hemimandible (for example for the height of a tooth, when only the top of a cusp was eroded) or based on the comparison of the eroded hemimandible with a complete hemimandible of a comparative specimen that is of similar size (for example for the length of the mandible). If for one of the 13 fossil North Sea specimens a parameter could not be measured, all other parameters were measured first and the probable identity of the specimen was established. The fossil specimen was also qualitatively compared to all comparative material (*Cuon alpinus*, *C. l. lupus* and *C. l. familiaris*) and for each parameter that could not be measured directly and for which the value was estimated based on comparison to a specimen from the comparative dataset it was described to which comparative specimen it resembled most and why it did not resemble to the other two comparative (sub)species. Subsequently, a comparative specimen (*Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* depending on the identity of the fossil North Sea specimen) with a very similar dimension for that specific parameter was chosen to compare the fossil North Sea specimen to and to make a reasonable estimate of the original value of the fossil specimen for that parameter. For example, the mandible length of a fossil North Sea specimen of which the anterior part of the hemimandible is missing can be reasonably estimated by comparing the specimen to another (complete) specimen with very similar dimensions. For some estimated values (such as the crown height) a 'lower boundary estimate' was given and for other estimated values a range was given. 'Lower boundary estimates' are an estimate of the minimum value that the fossil North Sea specimen had for that parameter. When a single comparative specimen with a very similar size as the fossil specimen was not present, two comparative specimens were used to estimate a minimum and maximum value for the fossil North Sea specimen: a comparative specimen that was slightly smaller and a specimen that was slightly larger were chosen to obtain a range for the fossil North Sea specimen. The original value of the fossil specimen was then certainly not smaller than the minimum and certainly not larger than the maximum value of that range. For each fossil North Sea specimen it will be mentioned in the corresponding paragraph in Chapter 4 when a value was estimated. Further details on these estimated values are given in the relevant paragraphs of Chapter 4.

#### *Comparing the 13 fossil North Sea specimens with the comparative material*

All 21 parameters were measured on all 100 Canidae specimens (appendix XIII). The parameters were measured on the mandibles of the 87 comparative *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* specimens to obtain the typical size interval of each parameter for each of these three (sub)species (for the quantitative parameters). All data resulting from the measurements on the comparative material are summarized in 5 statistics per parameter per comparative (sub)species: n (sample size), x (arithmetic mean), SD (sample standard deviation), MIN (smallest value that was measured) and MAX (largest value that was measured) (see box VI.1 and paragraph 2.2.4 for an explanation of these statistics and the SD). Arithmetic means, sample sizes and standard deviations of the three comparative (sub)species were individually compared to each other. The MIN and MAX were used to calculate two different ranges that indicate the typical size interval of each parameter for each of the three (sub)species: the sample range and population range (which are explained in 2.2.3 and 2.2.4). Ideally these ranges of the three (sub)species did not overlap. Subsequently, the values of the 13 fossil North Sea specimens were compared to these ranges and the 13 specimens could be identified based on a match or mismatch with the ranges of the three comparative (sub)species. Additionally to the quantitative parameters, qualitative descriptions of the morphology of the 13 fossil North Sea specimens in comparison to *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* are given. For all qualitative parameters (such as the mental foramina) that are not measured in millimeters the occurrence of the different options for each parameter was recorded and given in percentages for the comparative material (as will become clear in Chapter 4).

### 2.2.3 Measuring error: sample and specimen ranges

When measuring the same parameter several times on the same specimen, one will hardly ever obtain exactly the same value each time, as a result of a human measuring error. Arithmetic means, samples sizes and standard deviations are based on the entire samples of *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* and can thus be compared without further editing. The MIN and MAX on the contrary are only single values from a single specimen that will slightly vary when measuring again, but still represent the smallest and largest value of the entire samples of the three (sub)species. If we would compare the original, unedited MIN and MAX values of, for example, the parameter 'Distance' *a-d* of comparative *C. l. lupus* material (hypothetically 40 and 60 mm respectively) with a fossil North Sea specimen of 39 mm for *a-d*, we would conclude that this fossil specimen is probably not *C. l. lupus*, because it does not fall into that range. But this conclusion would be based on only a slight difference (1 mm) between the MIN and the value of the fossil specimen, while this difference also could have been the result of a small measuring error. We need to make a revised range that indicates the typical size interval of each parameter for each of the three (sub)species, but also includes the effect of the measuring error. To determine the margin of error a selection of ten parameters was repeatedly (10 times) measured on the same specimen (comparative recent *Canis l. lupus* specimen RMNH43492) (box 2.2).

**Box 2.2: Parameters that were used to determine the margin of error.** These 10 parameters were measured 10 times on comparative recent *Canis l. lupus* specimen RMNH43492.

- |   |  |
|---|--|
| 1. Length of the mandible ( <i>a-b</i> and <i>c-b</i> ).  | 6. Distance <i>e-e'</i> of the mandible.   |
| 2. Alveolar length of P <sub>1</sub> -M <sub>2</sub> .    | 7. Coronoid angle ( $\nu$ ).               |
| 3. Width of the mandible ( <i>i-i'</i> and <i>k-k'</i> ). | 8. Height of the crown of M <sub>1</sub> . |
| 4. Distance <i>h-h'</i> under M <sub>1</sub> .            | 9. Length of M <sub>1</sub> .              |
| 5. Distance <i>a-d</i> of the mandible.                   | 10. Breadth of M <sub>1</sub> .            |

This repeated measuring resulted in a dataset for specimen RMNH43492 of ten parameters with for each parameter ten similar values (appendix V). This dataset was summarized with the following statistics: x (arithmetic mean), MIN (smallest value that was measured), MAX (largest value that was measured), ΔMAX-MIN (the range of values that was obtained: minimum subtracted from maximum) and SD (population standard deviation) (appendix VI). For a given parameter, each of the ten values of specimen RMNH43492 include a slight measuring error and deviate slightly from the real value of RMNH43492 for that parameter. The real value is thus actually unknown, but reasonably assumed to be the arithmetic mean of all ten repeated measurements. The aim here is to extract the average measuring error from this dataset of repeated measurements, so that this error can be taken into account when comparing the 13 fossil North Sea specimens with the typical size ranges of the comparative (sub)species.

The average measuring error can be calculated using the standard deviation, which is defined as the average deviation from the arithmetic mean of a dataset (appendix VI). Calculating the standard deviation of the dataset of all repeated measurements gives the average measuring error, since the deviations of all ten repeated measurements from the arithmetic mean from this dataset are all slight measuring errors. Since the ten repeated measurements are all the arguments of the entire dataset and not only a sample of all repeated measurements, the STDEVP was used to calculate the standard deviation of this dataset of ten repeated measurements (see appendix VI for the formula that was used). The 2SD confidence interval, which is commonly reported as margin of error, was used as margin of error (table 2.1).

**Table 2.1: Margin of error for all quantitative parameters.** For the margin of error a confidence interval of 95% ( $2 \times \text{STDEVP}$ ) was used that was calculated based on the dataset of the 10 parameters that were measured 10 times on comparative recent *Canis l. lupus* specimen RMNH43492 (box 2.2 and appendix V). Note that the SDs of all parameters are given in mm, except that of the coronoid angle, which is given in degrees (these margins of error cannot be compared directly). The margins of error of these general parameters are based on the margins of error of the specific (sub)parameters given in box 2.2 and should be considered in perspective to the dimensions of the parameter.

Parameter	Margin of error
Coronoid angle $\nu$ (°)	3
Distance $e-e'$	1,83
Distance $a-d$	1,20
Length mandible $a-b$	0,98
Length mandible $c-b$	0,98
Length tooth	0,84
Width mandible $k-k'$	0,64
Height $h-h'$ of the mandible	0,28
Breadth tooth	0,22
Alveolar length tooth row	0,18
Diastema length	0,18
Width mandible $i-i'$	0,14
Height of the crown	0,14

Note that the parameters in table 2.1 are ordered according to the size of their margin of error, but that this does not necessarily mean that the coronoid angle was measured more inaccurately than the height of the crown. First of all, the coronoid angle was measured in degrees instead of millimeters and cannot be compared to the other parameters with respect to the margin of error. Secondly, the measuring inaccuracy of the mandible dimensions may seem larger than those of the teeth dimensions, but keep in mind that mandible dimensions are much larger than teeth dimensions and that a margin of error of 0.98 mm on a mandible length of 150 mm is comparable to a margin of error of 0.14 mm on a tooth length of 15 mm. Although the margins of error for distances  $e-e'$  and  $a-d$  are somewhat larger, the margins of error for all other parameters are below 1 mm and quite small.

The following example illustrates the use of the margin of error for the parameter 'Distance'  $a-d$  of comparative *C. l. lupus* material:

Subtracting the margin of error (1.20 mm) from the MIN value (40 mm) and adding it to the MAX value (60 mm) gives a range (38.8-61.2 mm) for the comparative *C. l. lupus* material, which hereby is termed 'sample range'. The margin of error was also added and subtracted to the single value of the hypothetical fossil specimen (39 mm), which results in a range of 37.8-40.2 mm. This range is hereby termed 'specimen range'. These two ranges now include the effect of the measuring error. The sample and specimen ranges were calculated for all MIN and MAX values of all three comparative (sub)species and all fossil North Sea specimens for all parameters (individual tables in Chapter 4 and appendix XIII). The specimen range indicates that, if the fossil specimen would be measured again, there is a 95% chance that the value falls again in the specimen range (37.8-40.2 mm in this example) (appendix VI). The same holds true for the smallest and largest *C. l. lupus* specimens (defining the MIN and MAX): if these specimens would be measured again, there is a 95% chance that the values for  $a-d$  would again fall in the sample range (that  $a-d$  could be as small as 38.8 mm or as large as 40.2 mm in this example). On the contrary, there is only a 2.3% chance that the fossil or comparative specimen would fall outside (below or above) this sample respectively specimen range. The margin of error or 95% confidence interval indicates that values that fall within the sample and specimen range can be the result of variation in measuring and only values that fall outside these ranges are not the result of measuring, but from natural variation and thus considered significant.

The initial conclusion for this hypothetical case was that the fossil specimen could not have been *C. l. lupus*, because it fell outside the *C. l. lupus* range, but now we see that this was an effect of the measuring error; if the MIN value and value of the fossil specimen would have been measured again they could fall anywhere in their specimen/sample ranges and thus possibly overlap. It is still very well possible that the fossil specimen is *C. l. lupus*, when taking into account the variations in measuring. The sample and specimen ranges, on the contrary to the original MIN-MAX range and value of the fossil specimen, thus include the effect of the measuring error and are more reliable to use in the comparison of the 13 fossil North Sea specimens to the comparative *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* material. If comparison of the specimen and sample

ranges still would not result in overlap between the two ranges, then the conclusion that the fossil specimen is not *C. l. lupus* (in this example) is more reliable than the initial conclusion based on the unedited range, because now the variation due to measuring is almost eliminated (only a 2.3% chance remains that the fossil specimen could still be *C. l. lupus* and that the difference of only 1 mm is the result of a measuring error).

In this example we see why was chosen for a 2SD confidence interval as margin of error instead of a 3SD confidence interval, apart from the fact that the 2SD interval is more commonly used (appendix VI): the difference between the confidence intervals (95% for 2SD and 99.7% for 3SD) is not very large (the confidence of the 2SD interval is already very large), but the use of the 3SD interval instead of the 2SD interval would make the specimen and sample ranges even larger. This would result in much more overlap between the typical size intervals of the comparative (sub)species and the fossil North Sea specimens and less fossil specimens that could be identified.

As was previously stated, sample and specimen ranges were calculated for all parameters for all comparative and fossil North Sea material, but the margin or error was only calculated for ten specific (sub)parameters. It was not necessary to calculate a margin of error for all individual quantitative parameters, because some parameters are very similar and are measured in an identical manner. For the quantitative parameters for which was not calculated a margin of error (compare box 2.1 and 2.2), the margin of error of a similar parameter (as given in table 2.1) is used as follows:

- The margin of error of the specific parameter 'Distance  $h-h'$  under  $M_1$ ' will be used for the distance  $h-h'$  under each mandibular tooth;
- The margin of error of the specific parameter 'Alveolar length of  $P_1-M_2$ ' will be used for all alveolar lengths and all diastema lengths that are measured, because the diastema length and the alveolar tooth row length are measured in an identical manner;
- The margin of error of the specific parameter 'Height of the crown of  $M_1$ ' will be used for the height of the crowns of all mandibular teeth;
- The margin of error of the specific parameter 'Length of  $M_1$ ' will be used for the length of all mandibular teeth;
- The margin of error of the specific parameter 'Breadth of  $M_1$ ' will be used for the breadth of all mandibular teeth.

Margins of error were calculated based on repeated measurements on a comparative recent *Canis l. lupus* specimen, but will be used on all material (recent and fossil *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* material and all 13 fossil North Sea specimens). The identity and age of the specimens will not be of influence on the measuring error.

## 2.2.4 Population ranges

The 21 parameters were measured on the mandibles of the three comparative (sub)species *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* to obtain the typical size interval of each parameter for each of these three (sub)species and to compare the specimen ranges of the 13 fossil North Sea specimens with. By applying this method one assumes that the samples of *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* are representative for the entire natural populations of these three (sub)species with respect to sample size, the different subspecies, localities and sex included. It is, however, highly unlikely that the *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* samples from the Naturalis museum represent all variation that is possible in nature. Although it is not possible to capture all natural variation in one dataset, it is possible to calculate the typical size interval of the three (sub)species for a given parameter that captures approximately 95% of all natural variation (2SD interval), reasonably assuming that the sample size is sufficiently large and that the sizes of the parameters used in this study are normally distributed (appendix VI). This 95% confidence interval around the arithmetic mean of the tree comparative (sub)species is hereby termed 'population range'. The population range was calculated for the three comparative (sub)species for each parameter using the STDEV function, because all 87 comparative specimens are clearly only samples of the entire natural *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* populations (appendix VI). All population ranges of the three (sub)species for all parameters can be found in appendix XIII.

Note that the population range is different from the sample range of the three samples: the sample range gives a range that includes all values that were actually measured in *this particular comparative dataset* (including the measuring error) and the population range gives the range of values that represents the size of 95% of *all specimens* of that (sub)species of its *entire natural population* for that particular parameter (appendix VI). Again taking the example of the parameter 'Distance  $a-d$ ' of comparative *C. l. lupus* material and a hypothetical fossil specimen, when the fossil specimen falls into the *C. l. lupus* sample range, it is very well possible that the specimen belongs to this subspecies, because in the particular dataset used for this

study *C. l. lupus* specimens were encountered with a similar value. When the fossil specimen falls just outside the sample range it is less likely that it belongs to *C. l. lupus*, because no *C. l. lupus* specimens were encountered in this comparative dataset with such a small or large value. The fact that the fossil specimen falls outside the sample range is very probably not the result of a measuring error, but of natural variation, since the margin of error is taken into account in the sample ranges. But, since the sample range does not represent all natural variation one cannot add a probability to the conclusion of how likely the fossil specimen is not *C. l. lupus*. The population range is also calculated based on this particular comparative dataset, but estimates all variation of the entire natural *C. l. lupus* population (assumed that the sample size is large enough). When the fossil specimen falls into the population range it is very likely that the specimen belongs to *C. l. lupus*, because 95% of all *C. l. lupus* specimens in the entire natural *C. l. lupus* population have values that fall within this range (appendix VI). When the fossil specimen falls outside (above or below) the population range we can add a probability to the conclusion that the specimen does not belong to the *C. l. lupus* subspecies, because only 2.3% of all specimens of the entire natural population have sizes for the parameter 'Distance' *a-d* lower than the PR- (population range MIN) and only 2.3% of all specimens of the entire natural population have sizes larger than the PR+ (population range MAX) (appendix VI). There is only a 2.3% chance that a fossil specimen that falls just outside the *C. l. lupus* population range still is a *C. l. lupus* specimen. When the fossil specimen falls far outside the population range, this chance reduces even more (figure VI.1). When the fossil specimen for example falls outside (below) the *C. l. lupus* population range, but into the *C. l. familiaris* population range for parameter 'Distance' *a-d*, then the chance that the fossil specimen is *C. l. familiaris* is much larger than that the specimen is *C. l. lupus* based on *a-d*. The statistical conclusion that the specimen is not *C. l. lupus* has a confidence level of 97.7% (100-2.3%, because the specimen is smaller than the population range and not smaller or larger, which coincides with a 95% confidence interval). But this conclusion is not entirely conclusive, because the chance that the fossil specimen is a *C. l. lupus* specimen with an extremely small value for 'Distance' *a-d* is small (2.3%), but still present. The sample ranges are thus an initial size indicator of the possible values for the parameters for the three comparative (sub)species and the population ranges add a statistical confidence interval of 97.7% to the conclusions. Also note that the population range can be smaller or larger than the sample range depending on the SD for each parameter.

As becomes obvious from the example above, the most conclusive statements about the identity of the 13 fossil North Sea specimens can be made when the fossil specimens fall outside instead of inside the sample and population ranges of *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris*, because in that case one or two (sub)species can be excluded as possibility with a 97.7% confidence interval. It is expected though, that the specimen ranges of the fossil specimens will fall within the sample and population ranges of two or even all three comparative (sub)species for certain parameters due to the natural continuum and similarities between species. Not all parameters will thus be conclusive about the identity of the fossil specimens. This is the reason why as many as possible parameters were measured: to be able to identify the fossil specimens based on a combination of parameters. The chance that a fossil specimen is, for example, *C. l. lupus* reduces with each parameter for which the fossil specimen falls outside the *C. l. lupus* population range. In pure statistics the chance that the fossil specimen is *C. l. lupus* would be: (the chance that the specimen falls outside the *C. l. lupus* population range (2.3%)) to the power of (the number of times that the specimen falls outside the *C. l. lupus* population range for a parameter) (as for example rolling a 6 with a dice two times in a row is  $(1/6)^2 = 1/36$ ). But the chance, that a fossil specimen that falls below the *C. l. lupus* population range for one parameter also falls below the *C. l. lupus* population range of another parameter, is not entirely random, because when a specimen has a small mandible length for example, other parameters (like 'Distance' *a-d*) will also be small. Thus, although, when a specimen falls outside the population ranges of several parameters, the chance that the specimen is still that (sub)species will not be reduced to a percentage as low as  $n \cdot 2.3\%$  (with  $n$  = the number of times that the specimen falls outside the population range of that (sub)species for that parameter), the chance that the fossil specimen belongs to that (sub)species is still reduced with every time that its specimen range falls outside the population range for that (sub)species.

All comparative material will thus be summarized with 9 statistics:  $n$ ,  $x$ , SD, MIN, MAX, SR- (sample range MIN), SR+ (sample range MAX), PR- (population range MIN) and PR+ (population range MAX) (appendix XIII). The arithmetic means and samples sizes are individually discussed, the single standard deviation is discussed with respect to its meaning that it indicates the variation within a (sub)species for a given parameter, but is also used to calculate the population range and the MIN and MAX are not discussed separately, but only used to calculate the sample ranges. The fossil North Sea specimens will be compared to the three comparative (sub)species using their specimen ranges. The original, single values of these specimens will only be used to plot the 13 fossil North Sea specimens in all figures (Chapter 4). The original 'average' values of the fossil specimens are plotted instead of their specimens' ranges to keep figures easily readable.

## 2.2.5 Comparative specimens from literature

Additionally to the values of all comparative specimens from the dataset created for this study, some values of *Cuon alpinus* and *C. l. lupus* specimens were found in literature (appendix IX). Values of the three comparative species for exactly the 21 parameters that are used in this study are sparse in literature and only for 6 of the 21 parameters values were found ('Alveolar length P<sub>1</sub>-M<sub>2</sub> and M<sub>1</sub>-M<sub>2</sub>', 'Mandible height *h-h*' under M<sub>1</sub>', 'Length of tooth M<sub>1</sub>' and the 'Breadth of teeth M<sub>1</sub> and M<sub>2</sub>'). However, all values of the *C. l. lupus* specimens that were found in literature fell into the sample and population ranges that were already calculated based on the comparative dataset of this study. Adding the values from literature would not change the minima and maxima of the sample and population ranges (and thus not influence the conclusions), but only involve recalculating and reinterpreting all sample and population ranges. These values were thus not used. For the six parameters mentioned above all *Cuon alpinus* values found in literature (both values that fell into the already existing sample and population ranges and values that fell outside these ranges) were added to the comparative dataset. Values that fall outside the already calculated sample and population ranges can possibly change the conclusions based on the comparison of the specimen ranges of the 13 fossil North Sea specimens with these ranges. Therefore new statistics were calculated for the comparative *Cuon alpinus* datasets for these six parameters (appendix IX). Additionally to the comparison of the specimen ranges of the 13 fossil North Sea specimens with the original sample and population ranges, the fossil specimens were compared to new sample and population ranges and a brief description and reinterpretation of the new results is given at the end of the corresponding paragraph for each of the six parameters in Chapter 4 (Results) and 5 (Discussion) respectively.

The reader must have noticed that the methods as explained in this chapter contain many assumptions. These assumptions will not go unnoticed and will be discussed in 5.1.





## 3 Canidae

In this chapter the Canidae taxonomy, as it is used in this study, is presented. Subsequently it is verified that the thirteen fossil North Sea specimens belong to the Canidae and that they do not belong to the genus *Vulpes* (foxes). Also is accounted for the choice of *Canis lupus lupus*, *Canis lupus familiaris* and *Cuon alpinus* as final comparative (sub)species.

### 3.1 Taxonomy

Box 3.1: Canidae taxonomy (based on Gray (1821) and Wilson and Reeder (2005))	
Order	Carnivora BOWDICH, 1821
Suborder	Caniformia KRETZOI, 1938
Family	Canidae FISHER, 1817
Subfamily	Caninae GRAY, 1821
Genus	<i>Canis</i> LINNAEUS, 1758
Species	<i>C. lupus</i> LINNAEUS, 1758, gray wolf
Subspecies	<i>C. l. lupus</i> LINNAEUS, 1758, Eurasian wolf
Subspecies	<i>C. l. familiaris</i> LINNAEUS, 1758, domestic dog
Genus	<i>Cuon</i> HODGSON, 1838
Species	<i>Cuon alpinus</i> PALLAS, 1811, dhole
Genus	<i>Vulpes</i> FRISCH, 1775
Species	<i>Vulpes vulpes</i> LINNAEUS, 1758, red fox

Box 3.1 gives the Canidae taxonomy as it is used in this thesis. Note that the subfamily Caninae is included in this taxonomy, but that this subfamily is actually equivalent to the recent Canidae, since of the three original subfamilies of the Canidae (Hesperocyoninae, Borophaginae and Caninae) only the Caninae subfamily (commonly referred to as canines) survived to present-day and led to all present-day canids (such as wolves, dogs, coyotes, jackals and foxes) (Tedford and Xiaoming, 2010). For all genera in the Caninae subfamily only the species and subspecies are given that are relevant for this study. Only for the genus *Canis* the genus name is abbreviated to *C.* in this report, to prevent confusion between the genera *Canis* and *Cuon*. In this study no distinction is made on subspecies level for the genera *Cuon* and *Vulpes*, because for the genus *Cuon*, *Cuon alpinus* is the only existing species (Anderson and Jones, 1984) and the validity of most of the 11 reported subspecies of *Cuon alpinus* is doubtful (Durbin et al., 2008). The genus *Vulpes* was only briefly used for comparison in this study and there was no need to distinguish on subspecies level for *Vulpes vulpes*.

General characteristics of wolf, dog, dhole and the red fox and their fossil mandibles can be found in the next paragraph and Chapter 4, where for each of the 21 parameters the typical appearance, values and features of these comparative (sub)species are described into detail.

### 3.2 Canidae material

In this paragraph is explained how it was known in the first place that the 13 fossil North Sea specimens belong to the Canidae and is accounted for the choice of *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* as final comparative (sub)species. The following questions will be answered:

- 1) How do we know that the fossil material from the North Sea belongs to the Canidae family?
- 2) Which Canidae species were part of the carnivore guild of Northwestern Europe during the Late Pleistocene?
- 3) Which of these species should be included in the comparative dataset?

#### How do we know that the fossil material from the North Sea belongs to the Canidae family?

Typical characteristics of the Canidae family and Caninae subfamily that can be recognized in hemimandibles are: unspecialized incisors, long and powerful canines, sharp premolars, well developed carnassials and a typical dental formula of 3/3-1/1-4/4-2/3 (with variation only in the molars: 1-2/2 in *Speothos* (with a total of 38-40 teeth), to 3-4/4-5 in *Otocyon* (with a total of 46-50 teeth)) (Anderson and Jones, 1984). The first common level of *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* in the Canidae taxonomy is the Caninae subfamily and the Canidae family. Since all the 13 fossil North Sea specimens possess these typical Caninae/Canidae characteristics (for as far as can be determined, appendix I) and possess a typical Canidae morphology and size of the hemimandible, they are all included in the Canidae. We know now that the 13 fossil North Sea specimens are Canidae specimens from the North Sea and that they most probably have a Late Pleistocene age (Introduction). To be able to identify these hemimandibles

on genus, species and subspecies level we need to compare them to mandibles of all possible Canidae species that were part of the carnivore guild of Northwestern Europe during the Late Pleistocene.

### **Which Canidae species were part of the carnivore guild of Northwestern Europe during the Late Pleistocene?**

All species of the Canidae family that have a different dental formula than the 13 fossil Canidae hemimandibles (such as *Otocyon*) and/or could not reasonably have lived in the North Sea area during the Late Pleistocene, because they evolved elsewhere, did not occur in Europe during the Late Pleistocene or were already extinct by that time (information based on Canidae diagnoses from Anderson and Jones (1984), Nowak (1999) and Romer (1966)) were excluded as possible comparative species. (Sub)species that remain are: *C. l. lupus* (Eurasian wolf), *C. l. familiaris* (dog), *Cuon alpinus* (dhole) and the genus *Vulpes* (true foxes). A brief comparison of the 13 fossil North Sea hemimandibles with species of these three genera, could already reduce the comparative dataset to only three (sub)species:

### **Which of these species should be included in the comparative dataset?**

It is known that true foxes can be distinguished from members of the genus *Canis* (and thus wolf and dog) by their smaller size, among other things (Wilson and Reeder, 2005). To see whether *Vulpes* can be excluded from the comparative dataset, the 13 fossil North Sea hemimandibles and comparative *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* specimens were qualitatively compared to several recent specimens of the largest species of the true foxes, *Vulpes vulpes* L. (Canidae collection deposited in NCB Naturalis).

#### *Mandible*

The first very clear observation, when comparing *Vulpes vulpes* specimens with the 13 fossil North Sea specimens, is that the mandibles of foxes are very small. Parameters such as the length, width and height of the mandible and distances *a-d* and *e-e'* do not need to be measured to see that the largest fox specimens are much smaller than specimen NMR90 (one of the smallest of the fossil North Sea specimens), all other fossil North Sea specimens and all comparative *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* specimens. The ratio of the height of the teeth to the mandibular body below is approximately 1/3 (teeth) to 2/3 (mandibular body) in foxes, while in all fossil North Sea specimens and all comparative *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* specimens the height of the mandibular body below the teeth is much larger. Mandibles of fox are not only smaller with respect to mandibular height, but also to width and as a result appear much more fragile than all other material. Both subspecies of *C. lupus* have larger heights and widths of the mandibular body. Also *Cuon alpinus* specimens, which are in general smaller than *Canis* specimens, are larger and much sturdier than fox: the width of *Cuon alpinus* mandibles is much thicker compared to the height than the width of fox mandibles. All observations of the general appearance of the mandible indicate that even the largest *Vulpes* species (*Vulpes vulpes*, Wilson and Reeder (2005)) is relatively small and fragile and that all fossil North Sea specimens and all comparative *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* specimens have larger, longer, wider and thicker mandibles.

#### *Teeth*

Teeth of *Vulpes vulpes* specimens are also much smaller than any teeth that are present in the fossil North Sea specimens and all comparative *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* specimens. The P<sub>4</sub> of fox specimens possesses several dental features that are different than in *Cuon*, *Canis* and all fossil North Sea specimens: the protoconid is centered and a posterior cusp is aligned on the buccal side of the P<sub>4</sub> (these two cusps are aligned like the para- and protoconid are aligned in a typical *Canis* M<sub>1</sub>, box III.3 and fig. III.1), while in *Cuon*, *Canis* and all fossil North Sea specimens the protoconid and posterior cusp of the P<sub>4</sub> are both aligned and centered (box IV.4 and 4.4.4); distal of the posterior cusp a well pronounced cingulum is present, where the cingulum is less pronounced in *Cuon*, *Canis* and all fossil North Sea specimens; the protoconid of a fox P<sub>4</sub> possesses a weak metaconid-like cusp on its labial side (as is the case in a typical *Canis* M<sub>1</sub>, fig. III.1), while in *Cuon*, *Canis* and all fossil North Sea specimens this is never the case in the P<sub>4</sub> (box IV.4 and 4.4.4). The M<sub>1</sub> of fox specimens also possesses several dental features that are different than in *Cuon*, *Canis* and all fossil North Sea specimens: the M<sub>1</sub> of a fox possesses a para- and protoconid along the buccal edge of the tooth, while these two cusps are centered in *Cuon*, *Canis* and all fossil North Sea specimens (fig. III.1 and 4.4.4); the metaconid is very pronounced as a little bulge on the labial side of the tooth (this cusp is even more pronounced than is the case in *Cuon*, *Canis* and all fossil North Sea specimens); a fox M<sub>1</sub> possesses a very large talonid basin with 3 or 4 cusps: a clear hypo- and entoconid, hypoconulid and an extra cusp between the entoconid and metaconid on the labial side of the tooth, while the maximum number of cusps that was encountered on an M<sub>1</sub> of *Cuon*, *Canis* and all fossil North Sea specimens is 5 (4.4.4 and plate 4.2). The P<sub>4</sub> and M<sub>1</sub> of *Vulpes vulpes* specimens are thus relatively broader and possess a larger talonid basin, with more cusps.

All evidence of the qualitative comparison indicates that the 13 fossil North Sea specimens are very different from typical *Vulpes vulpes* specimens. If the selection of *Vulpes vulpes* specimens that was used for this comparison is representative for this species (which it probably is), we can conclude that the 13 fossil North Sea specimens clearly do not belong to *Vulpes vulpes* (or other species of the genus *Vulpes* (including *Vulpes lagopus*, the Arctic fox, formerly put in the genus *Alopex*), because *Vulpes vulpes* is smaller and more fragile than all fossil North Sea specimens, while it is the largest *Vulpes* species). The final remaining (sub)species that will be included in the comparative dataset are:

*C. l. lupus* LINNAEUS, 1758, wolf

*C. l. familiaris* LINNAEUS, 1758, dog

*Cuon alpinus*, PALLAS, 1811, dhole



**Figure 3.1: Wolf.** From: <http://www.flickr.com> by forbesimages.



**Figure 3.2: German shepherd dog.** One of the many dog breeds.  
From: <http://www.flickr.com> by anetaelk.



**Figure 3.3: Dhole.**  
From: <http://www.flickr.com> by A.J. Haverkamp.



## 4 Results

In this chapter all results of the comparison of the thirteen fossil North Sea specimens with the comparative datasets of *Canis lupus lupus*, *Canis lupus familiaris* and *Cuon alpinus* for all 21 morphological and osteometrical parameters are presented into detail.

### 4.1 Mandible length

#### 4.1.1 Length mandible *a-b* and *c-b*

##### 4.1.1.1 Results comparative material

For all values see both table 4.1 and fig. 4.1 below unless stated otherwise.

**x** With 172 mm *C. l. lupus* has on average the biggest mandible length (*a-b*, fig. IV.1), followed by *C. l. familiaris* (135 mm) and *Cuon alpinus* (128.47 mm) (table 4.1). *C. l. lupus* mandibles clearly are larger than *Cuon alpinus* and *C. l. familiaris* mandibles, of which the means lie closer together than the means of both *Canis* species. Values are very similar for *c-b*.

**SD vs. n** *C. l. familiaris* shows the greatest variation in mandible length (SD of 18.5 mm and largest range in fig. 3.1), while this species also has the greatest sample size (n 41). *C. l. lupus*, the species with the lowest sample size (n 14), shows more variation (SD 12.6 mm) than *Cuon alpinus* (SD 7.27 mm), which has a much greater sample size (n 27) than *C. l. lupus* (table 4.1). Values are very similar for parameter *c-b* and the same peculiar trend can be seen.

**Sample ranges** For all values of the sample ranges see table 4.1. For parameter *a-b* the ranges of *C. l. lupus* and *Cuon alpinus* overlap with 4.32 mm (see also the *C. l. lupus* SR- and *Cuon alpinus* SR+ data points in fig. 4.1). For *c-b* the amount of overlap is much less (0.93 mm). *Cuon alpinus* specimens plot in the lower parts of fig. 4.1, while *C. l. lupus* plots in the higher regions for both *a-b* and *c-b*. This observation is in accordance with the statement of Pérez Ripoll et al. (2010), that a characteristic feature of *Cuon alpinus* is that the mandibles are shorter than mandibles of *Canis lupus*. *C. l. familiaris* has the largest range (both *a-b* and *c-b*) and plots from lower than the *Cuon alpinus* minimum to slightly larger than the mean *C. l. lupus* mandible length. A distinction can be made within the *C. l. familiaris* group, separating the fossil specimens from the Netherlands from the recent specimens from Suriname (fig. VII.1). Most recent specimens plot in the lower part of fig. VII.1 (103-125 mm), although this recent group is very varied; its specimens form the minimum and maximum of the *C. l. familiaris* range. The recent group also includes some specimens from the Netherlands, but the majority is from Suriname. The fossil specimens from the Netherlands plot together in a data cloud in the upper part of the *C. l. familiaris* range, starting at a mandible length of approximately 125 mm (fig. VII.1). Although this distinction between the two *C. l. familiaris* groups is not very clear, since specimens of both groups occur in a large part of the entire *C. l. familiaris* range, the fossil specimens from the Netherlands plot together in a data cloud and are not randomly scattered over the entire *C. l. familiaris* range. García and Arsuaga (1998) state that *Cuon alpinus* mandibles are short when compared to typical members of the entire genus *Canis*, but when looking at the entire *C. l. familiaris* range, *Cuon alpinus* and *C. l. familiaris* are the species that are much more similar in mandible length instead of *C. l. familiaris* and *C. l. lupus*. When only looking at the fossil specimens of *C. l. familiaris*, *Cuon alpinus* is indeed shorter than *Canis*. The data points (specimens) of *C. l. familiaris* plot quite evenly over its range: the entire range has the same density of specimens (fig. 4.1). *C. l. familiaris* specimen 7028 causes the only bigger 'gap' in data points, which is the specimen with the largest mandible length (on average 14 mm larger than the second biggest specimen). The *C. l. lupus* specimens that have the smallest (*lupus-m*), respectively the biggest (*lupus-c*) mandible lengths are also separated from the rest of the *C. l. lupus* data cloud by quite a few millimeters (16 mm respectively 14 mm) (see also appendix XIII for these comparative specimens). Data points in the *Cuon alpinus* range are distributed a little less evenly. There are two bigger 'gaps' in the data cloud: *Cuon alpinus* specimen 20551 has a mandible length of 9 mm smaller than the second smallest specimen and *Cuon alpinus* specimens 945 and *cuon-a-sib* are the two largest specimens, with a mandible length of respectively 8 mm and 14 mm larger than the third largest specimen (fig. 4.1).

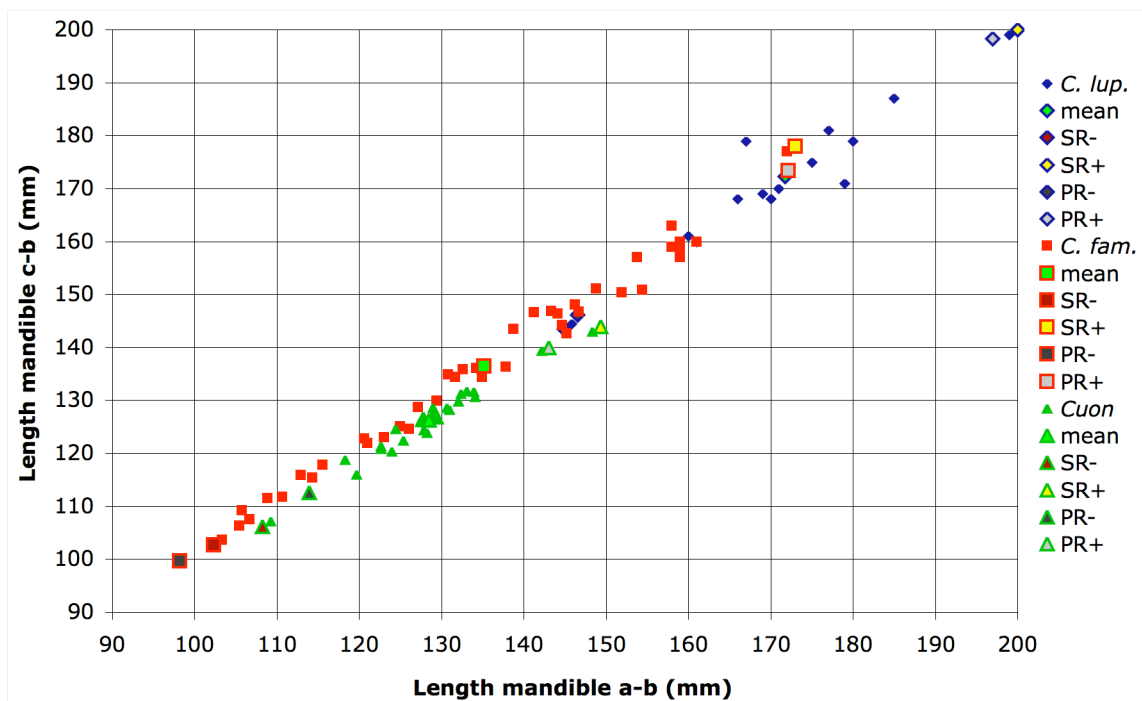
**Population ranges** For all values of the population ranges see table 4.1. For both parameters *C. l. lupus* and *Cuon alpinus* ranges are nicely separated: for *a-b* by 3.99 mm and for *c-b* by 5.99 mm (see also the *Cuon alpinus* PR+ and *C. l. lupus* PR- data points in fig 4.1). *C. l. familiaris* ranges still overlap greatly with both the *Cuon alpinus* and *C. l. lupus* ranges (fig 4.1: the *C. l. familiaris* PR- data point plots well below the *Cuon alpinus* PR- for both *a-b* and *c-b* and the *C. l. familiaris* PR+ is just as large as the *C. l. lupus* mean for *a-b* and even larger than the *C. l. lupus* mean for *c-b*).

**Trend lines** *C. l. lupus* shows slightly more variation in *c-b* than in *a-b*, while *Cuon alpinus* and *C. l. familiaris* have slightly less variation in *c-b* than in *a-b* (SD values in table 4.1 and fig. VIII.1). But in general the two parameters are quite similar in values and data point plot on a nice linear line. Parameters *a-b* and *c-b* are

well comparable. A prominent feature in fig. 4.1 is that *Cuon alpinus* values are positioned below *C. l. familiaris* values (for a fixed value of *a-b* *Cuon alpinus* values always have a slightly lower value for *c-b* than *C. l. familiaris*) (trend lines in fig. VIII.1). Trend lines of *C. l. familiaris* and *C. l. lupus* on the contrary are a continuation of each other. Two *C. l. lupus* specimens (RMNH43490 and *lupus-e*) deviate a little from the *C. l. lupus* trend line: RMNH43490 shows a low value for *c-b* compared to *a-b* and *lupus-e* shows a high value for *c-b* compared to *a-b*.

**Table 4.1: Statistics of the parameters ‘Length mandible’ *a-b* (left) and *c-b* (right) of the comparative material (in mm).** Sample size: the amount of specimens that was measured for that comparative (sub)species for that specific parameter (see also box VI.1). Note that this sample size can differ from the original sample sizes of *C. l. lupus* (18), *C. l. familiaris* (42) and *Cuon alpinus* (27), because not all parameters could be measured on all specimens due to erosion. Sample mean: the mean value for that comparative (sub)species for that specific parameter (see also box VI.1). Standard deviation: the amount of variation in that comparative (sub)species for that specific parameter (STDEV, box VI.1). Minimum and maximum: the smallest respectively largest value that was measured on a specimen of that comparative (sub)species for that specific parameter. Sample range MIN and MAX indicate the entire range of values for that specific parameter that was encountered in the samples of the comparative material including the effect of the measuring error (2.2.3). Population range MIN and MAX indicate the range of values for that specific parameter in which 95% of all specimens of the entire natural populations of the comparative material lies (2.2.4).

Statistics	Length mandible <i>a-b</i>			Length mandible <i>c-b</i>		
	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>
Sample size (n)	14	41	27	14	41	27
Sample mean (x)	172	135	128,47	172	137	126,30
Standard deviation (SD)	12,6	18,5	7,27	13,0	18,4	6,86
Minimum (MIN)	146	103	109,23	144	104	107,20
Maximum (MAX)	199	172	148,34	199	177	142,95
Sample range MIN	145	102	108,25	143	103	106,22
Sample range MAX	200	173	149,32	200	178	143,93
Population range MIN	147	98,2	113,92	146	99,6	112,58
Population range MAX	197	172	143,01	198	173	140,01



**Figure 4.1: Scatter plot of parameters ‘Length mandible’ *a-b* vs. *c-b* for the comparative material (in mm).** All individual specimens of all three comparative (sub)species are plotted (closed blue diamonds for *C. l. lupus*, closed red squares for *C. l. familiaris* and closed green triangles for *Cuon alpinus*), as well as the means (green filling), sample ranges (red filling for the minimum value (SR-) and yellow filling for the maximum value (SR+)) and population ranges (dark gray filling for the minimum value (PR-) and light gray filling for the maximum value (PR+)) (2.2.3, 2.2.4 and table 4.1).

#### 4.1.1.2 Results fossil North Sea material

For 12 of the 13 fossil North Sea specimens, parameters *a-b* and *c-b* could not be measured directly on the specimen to obtain the exact value of that specific specimen, because these specimens are not complete anymore (angular process, condyle and/or the most anterior part of the mandible are missing, appendix I). But for all of these specimens a large enough mandible part remained to make a reasonable estimate of the mandible lengths (2.2.2). Thus keep in mind that for the following fossil North Sea specimens (except specimen 2104) the specimen ranges are estimates based on specimens of the comparative material (indicated by a \* in appendix XIII).

##### Specimen 534

Specimen 534 is a posterior part of a hemimandible, thus parameters *a-b* and *c-b* could not be measured directly on this specimen (appendix I). From other results (teeth int. al.) was already known that specimen 534 very probably was not *Cuon alpinus* (appendix XIII). Moreover specimen 534 is a quite large mandible part: it is bigger in size than all comparative *C. l. familiaris* and *Cuon alpinus* specimens. Therefore two comparative *C. l. lupus* specimens (*lupus-c* and *lupus-g*) were used to estimate the mandible length for this fossil North Sea specimen. *Lupus-g* was used as minimum value: the mandible of specimen 534 was certainly not shorter than this value and probably longer. *Lupus-c* was used as maximum value: mandible of specimen 534 was certainly not longer than this value and probably shorter.

The hemimandible of specimen 534 is much longer than *C. l. familiaris* and *Cuon alpinus* mandibles: the specimen range falls entirely outside (above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* (table 4.2 and fig. 4.2). For *c-b* the minimum value of 534 coincides with the maximum value of the *C. l. familiaris* sample range, but the specimen range is mostly larger than the *C. l. familiaris* sample range. Specimen 534 falls entirely within the sample range of *C. l. lupus* and even plots in the upper part of this range for both *a-b* and *c-b*. The specimen range of 534 coincides for most part with the *C. l. lupus* population range, but also partly is bigger than the maximum value of *C. l. lupus* for both *a-b* and *c-b*. The mean value of specimen 534 for *a-b* (190 mm, appendix XIII) is most similar to the average *C. l. lupus* specimen (with a distance of 17.7 mm between the two mean values) and very dissimilar to the average *C. l. familiaris* (54.3 mm) and *Cuon alpinus* (61.0 mm) specimen (see appendix XIII for all mean values). Values are very similar for *c-b* and will not be discussed separately. Specimen 534 plots exactly on the *C. l. lupus* trend line, far away from the *Cuon alpinus* and *C. l. familiaris* data clouds (VIII.1).

##### Specimen 535

Specimen 535 misses a great part of its mandible, thus its values for *a-b* and *c-b* had to be estimated (appendix I). From other results (teeth int. al.) was already known that specimen 535 very probably was not *Cuon alpinus*. 535 is also a quite large specimen: it is bigger in size than all comparative *Cuon alpinus* and almost all *C. l. familiaris* specimens. Qua appearance 535 looks most similar to *C. l. lupus*, therefore 535 was compared to several *C. l. lupus* specimens. The values of *a-b* and *c-b* of the most similar specimen (*lupus-d*) were used as estimate for specimen 535.

The specimen range of 535 falls entirely within the sample and population ranges of *C. l. lupus* and *C. l. familiaris* for both *a-b* and *c-b*, although 535 is quite large compared to the last mentioned species (table 4.2 and fig. 4.2). Hemimandible 535 is much larger than the sample and population ranges of *Cuon alpinus* for both *a-b* and *c-b*. The mean value of specimen 535 for *a-b* (171 mm) is most similar to the average *C. l. lupus* specimen (with a distance of only 0.8 mm between the two mean values) and very dissimilar to the average *C. l. familiaris* (35.8 mm) and *Cuon alpinus* (42.5 mm) specimens (appendix XIII). Values are similar for *c-b*. Specimen 535 plots very close to the *Canis* trend lines in the upper part of fig. VIII.1.

##### Specimen 667

Specimen 667 appears quite small, but does not look like *Cuon alpinus* (it is less sturdy) and other parameters (teeth int. al.) already indicated that 667 is indeed probably not *Cuon alpinus* (appendix I). The specimen is smaller than all comparative *C. l. lupus* material and compares best to *C. l. familiaris* qua overall appearance. Comparative *C. l. familiaris* specimen 18051 is most similar to 667 in size and was used to estimate the values for *a-b* and *c-b* for this fossil North Sea specimen.

Specimen 667 falls entirely within the (fossil part of the) *C. l. familiaris* sample and population ranges for both *a-b* and *c-b*. This specimen also falls (partially) within the sample ranges of *C. l. lupus* and *Cuon alpinus*: the upper value of the specimen range of 667 overlaps with 0.60 mm with the lower part of the *C. l. lupus* sample range for *a-b*, but the remaining 1.96 mm of the 667 range falls below the *C. l. lupus* range and there is slight overlap of 667 with the *Cuon alpinus* range (0.68 mm), although most part of the 667 range (1.28 mm) falls outside (above) the *Cuon alpinus* range (table 4.2 and fig. 4.2). For both *a-b* and *c-b* the specimen range of 667 falls entirely outside the population ranges of *C. l. lupus* (below) and *Cuon alpinus* (above). The mean

value of specimen 667 for *a-b* (144.62 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 9.4 mm between the two mean values) less similar to the average *Cuon alpinus* (16.2 mm) and most dissimilar to the *C. l. lupus* mean (27.2 mm) (appendix XIII). Values are very similar for *c-b*. Specimen 667 plots very close to the *C. l. familiaris* trend line and further away from the *Cuon alpinus* trend line (fig. VIII.1).

### **Specimen 1683**

Specimen 1683 is a quite large hemimandible and is bigger than all comparative *C. l. familiaris* and *Cuon alpinus* material (appendix I). Looking at the results of other parameters (teeth int. al.) this specimen is very probably a *Canis* specimen and not *Cuon alpinus*. The most similar mandible is *lupus-c* (the largest comparative *C. l. lupus* specimen), but specimen 1683 is even more heavily built, with a greater width and height of the mandible. *Lupus-c* was used to estimate the minimum values for 1683: the real values might even have been slightly bigger.

The specimen range of 1683 falls entirely outside (above) the sample and population ranges for *Cuon alpinus* and *C. l. familiaris*, and even just above the *C. l. lupus* population range for both *a-b* and *c-b* (table 4.2 and fig. 4.2). Specimen 1683 falls entirely within the *C. l. lupus* sample ranges. Specimen 1683 is extremely large compared to all ranges and the mean value of 1683 for *a-b* (199 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 27.2 mm between the two mean values) and significantly less similar to the average *C. l. familiaris* (63.8 mm) and *Cuon alpinus* (70.5 mm) specimen (appendix XIII). Values are very similar for *c-b*. Specimen 1683 plots exactly on the *C. l. lupus* trend line, far away from the *C. l. familiaris* and *Cuon alpinus* data clouds (fig. VIII.1).

### **Specimen 2103**

Specimen 2103 is average sized and qualitatively appears bigger than all *Cuon alpinus* comparative material (appendix I). Moreover other results (teeth int. al.) already indicated that 2103 probably is not *Cuon alpinus*. Qua overall appearance it does not compare well to *C. l. lupus* (it looks more fragile like *C. l. familiaris*) and it is also smaller than most *C. l. lupus* specimens. 2103 Compares best to *C. l. familiaris* specimens qua overall appearance and size. The mandible length of 2103 was probably slightly bigger than comparative *C. l. familiaris* specimen 18051 and similar in size to specimen 33824. Specimen 18051 was used as minimum and 33824 as maximum value for the specimen range of 2103.

The specimen range of 2103 overlaps partially (for the largest part) with the *C. l. lupus* sample range for *a-b*, although it plots on the lower part of that range (table 4.2 and fig. 4.2). The fossil specimen falls entirely within the *C. l. lupus* sample range for *c-b*. Specimen 2103 falls outside (above) the *Cuon alpinus* sample range for most part of its specimen range for both *a-b* and *c-b* (overlap is 5.32 mm for *a-b* and only 0.93 mm for *c-b*, while 12.68 mm for *a-b* and 17.07 mm for *c-b* fall outside the *Cuon alpinus* ranges). For both *a-b* and *c-b* the specimen range of 2103 falls partly outside (below) the population range of *C. l. lupus*, but for most part within this range. 2103 falls entirely outside (above) the *Cuon alpinus* population ranges. Specimen 2103 falls well within the (fossil part of the) *C. l. familiaris* sample and population ranges for both *a-b* and *c-b* (fig. VII.1). The mean value of specimen 2103 for *a-b* (153 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 17.6 mm between the two mean values) and *C. l. lupus* specimen (19.0 mm). 2103 is least similar to the average *Cuon alpinus* specimen (24.3 mm) (appendix XIII). Values for *c-b* are very similar. Specimen 2103 lies close to the *Canis* trend lines and is situated above the *Cuon alpinus* data cloud (fig. VIII.1).

### **Specimen 2104**

Specimen 2104 is average sized and very similar in size and appearance to specimen 2103 and thus *C. l. familiaris* specimens, although 2103 has a slightly larger mandible length (appendix I). Parameters *a-b* and *c-b* could be measured directly on specimen 2104, thus no qualitative comparison to other specimens was needed to obtain the values for these parameters.

The specimen range of 2104 falls (partially) outside (below) the *C. l. lupus* sample ranges (for *c-b* specimen 2104 falls for most part (1.77 mm) in the *C. l. lupus* range, while only 0.22 mm falls outside that range) and entirely outside (below) corresponding population ranges (table 4.2 and fig. 4.2). Specimen 2104 falls for most part (1.15 mm) outside (above) the *Cuon alpinus* sample range for *c-b*, with only 0.81 mm inside that range and entirely outside corresponding population range. Specimen 2104 falls entirely within the sample and population ranges of *Cuon alpinus* for *a-b* and entirely within the (fossil part of the) *C. l. familiaris* sample and population ranges for both parameters. The mean value of specimen 2104 (141.80 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 6.62 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (13.33 mm) and least similar to *C. l. lupus* (30.0 mm) for *a-b* (appendix XIII). Values are comparable for *c-b* (except that 2104 is even less similar to *Cuon alpinus* (17.46



mm) for this parameter). Specimen 2104 lies exactly on the *C. l. familiaris* trend line, 'above' all *Cuon alpinus* data points (fig. VIII.1).

### Specimen 2196

Specimen 2196 is one of three largest fossil North Sea specimens and is bigger than all comparative *C. l. familiaris* and *Cuon alpinus* material (appendix I). Results of other parameters (teeth int. al.) indicated that this specimen is very probably a *Canis* specimen and not *Cuon alpinus* and qua appearance 2196 looks far too large and robust to be a *Cuon alpinus* or *C. l. familiaris* specimen. Specimen 2196 compares very well to comparative *C. l. lupus* specimen *lupus-c*, the same specimen that was used to estimate the specimen range of fossil North Sea specimen 1683. Qualitative comparison of specimen 2196 and 1683 indicates that these two specimens probably had very similar mandible lengths. A qualitative difference between 2196 and 1683 is that 1683 was slightly more heavily built than *lupus-c*, where 2196 is not. This specimen compares better to *lupus-c* than 1683: values are likely to have been very similar. *Lupus-c* was used to estimate the specimen range of 2196, with the result that the specimen range and thus all results are identical to specimen 1683. These results will not be repeated here (see results at 1683).

### Specimen 2329

Specimen 2329 is a quite large hemimandible that is very similar in appearance and size to specimen 534 (appendix I). All qualitative descriptions given for specimen 534 also hold true for specimen 2329 and the same comparative *C. l. lupus* specimens (*lupus-c* and *lupus-g*) that were used to estimate the specimen range of specimen 534 were also used to estimate the minimum and maximum value for 2329. As a result all results described at specimen 534 also hold true for specimen 2329 and will not be repeated here (see 534).

### Specimen 2620

Specimen 2620 is the third specimen of the three largest fossil North Sea specimens and is just as 2196 very similar to specimen 1683 and thus *lupus-c* (which was used to estimate the specimen range for this specimen) (appendix I). Specimen 2620 appears to be slightly more heavily built than *lupus-c*, just as specimen 1683. All qualitative descriptions and results for this specimen are the same as for 2196 and 1683 and can be found in corresponding paragraphs.

### Specimen 3219

The specimen range of 3219 was based on the same comparative *C. l. familiaris* specimens as were used to estimate the specimen range for specimen 2103. Specimen 3219 indeed compares very well to 2103 (appendix I). All qualitative descriptions and results for this specimen are the same as for specimen 2103 and can be found in corresponding paragraph.

### Specimen 3293

Specimen 3293 is larger than all comparative *C. l. familiaris* and *Cuon alpinus* material (appendix I). Results of other parameters (teeth int. al.) indicated that this specimen is very probably a *Canis* specimen and not *Cuon alpinus*. Specimen 3293 is a large, thick and robust hemimandible, unlike *C. l. familiaris*. Qua appearance specimen 3293 is most similar to comparative specimen *lupus-g*, although its mandible length was probably slightly bigger. Specimen *lupus-g* was used to estimate the specimen range of this fossil North Sea specimen.

For both parameters *a-b* and *c-b* the specimen range of 3293 falls well within the *C. l. lupus* sample and population ranges and entirely outside (above) the *C. l. familiaris* and *Cuon alpinus* sample and population ranges (table 4.2 and fig. 4.2). For *c-b* the minimum value of the specimen range of 3293 coincides with the maximum value of the *C. l. familiaris* sample range, but the rest of the specimen range is larger than the *C. l. familiaris* sample range. The mean value of specimen 3293 (180 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 8.22 mm between the two mean values), and significantly less similar to the average *C. l. familiaris* (44.8 mm) and *Cuon alpinus* (51.5 mm) specimens (appendix XIII). Values are very similar for *c-b*. Specimen 3293 plots very close to the *C. l. lupus* trend line, above the *C. l. familiaris* and *Cuon alpinus* data clouds (fig. VIII.1).

### Specimen NMR89

The mandible of NMR89 is larger than all comparative *Cuon alpinus* specimens (appendix I) and results of other parameters (teeth int. al.) indicated that this specimen is very probably a *Canis* specimen and not *Cuon alpinus*. Qua overall appearance this specimen looks very similar to comparative *C. l. lupus* specimen RMNH92: the hemimandibles have almost identical heights, widths (probably also lengths) and ratios of the ramus versus the mandible. Although a *C. l. lupus* specimen compared best to NMR89, qualitatively it is hard to tell whether this hemimandible is more similar to *C. l. lupus* or *C. l. familiaris*: the hemimandible is not

extremely thick and robust as typical *C. l. lupus* specimens but neither thinner and more fragile like typical *C. l. familiaris* specimens. Specimen RMNH92 was used to estimate the specimen range for NMR89.

For both parameters *a-b* and *c-b* the specimen range of NMR89 falls within the *C. l. lupus* and *C. l. familiaris* (fossil part) sample and population ranges and outside (above) the *Cuon alpinus* sample and population ranges (table 4.2 and fig. 4.2). The mean value of specimen NMR89 (160 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 11.8 mm between the two mean values) and less similar to the average *C. l. familiaris* (24.8 mm) and *Cuon alpinus* (31.5 mm) specimens (appendix XIII). Values are very similar for *c-b*. NMR89 plots exactly on the *Canis* trend lines, above the *Cuon alpinus* data cloud (fig. VIII.1).

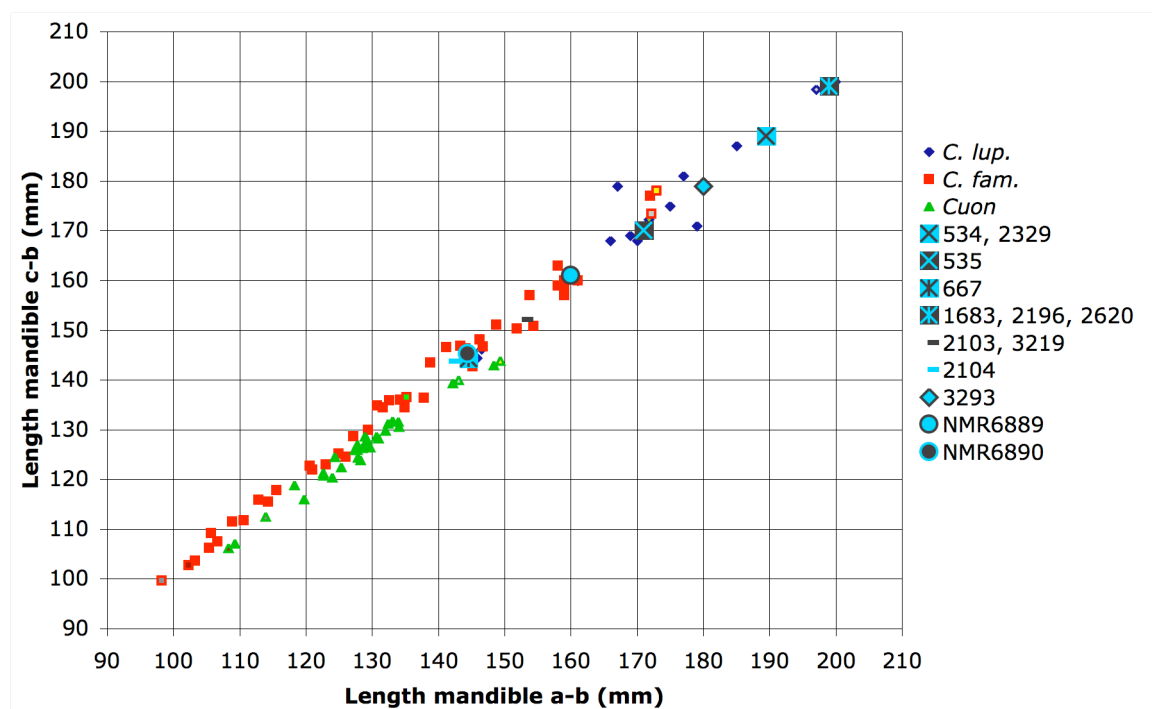
### Specimen NMR90

The specimen ranges for NMR90 were estimated from two *C. l. familiaris* specimens (specimen 18051 and 34601 of the comparative material). NMR90 was compared to many *Cuon alpinus* specimens, but did not resemble any of them. When the size of the ramus of NMR90 coincided with a *Cuon alpinus* specimen, the mandible of NMR90 was always much longer than the mandible of the *Cuon alpinus* specimen. A large anterior part of the mandible is missing, but this could still be told from the position of the molar and premolar: the  $M_1$  and  $P_4$  of NMR90 were in all cases offset towards mesial by at least the length of half an  $M_1$  compared to the *Cuon alpinus* specimen. Even when the size of the ramus of NMR90 was (much) smaller than that of the comparative *Cuon alpinus* specimen, the mandible of NMR90 still was longer than the *Cuon alpinus* specimen in all cases. This comparison indicates that specimen NMR90 has other mandible ratios than *Cuon alpinus* (4.2.5). NMR90 was also compared to many *C. l. lupus* specimens, but in all cases these mandibles were much larger and much more robust than NMR90, which is smaller and appears more fragile. *C. l. familiaris* appeared to be the most appropriate species to compare NMR90 with. Ratios of ramus size and mandible length are much more alike for NMR90 and *C. l. familiaris* and *C. l. familiaris* also appears more fragile, like NMR90. Comparing the ramus size and mandible length (position of  $M_1$  and  $P_4$ ) NMR90 is most similar to specimens *C. l. familiaris* 18051 and 34601 of the comparative material. NMR90 appears to be slightly bigger than specimen 18051 and comparable in size to 34601, although qualitatively the difference is hard to tell. To obtain a size indication for the mandible length of NMR90 the values of those two specimens were taken as minimum and maximum value.

For *a-b* the specimen range of NMR90 partly falls within the sample range of *C. l. lupus* (the upper value of the range of NMR90 overlaps with 0.60 mm with the lower part of the *C. l. lupus* range and the remaining 1.87 mm of the NMR90 range falls below the *C. l. lupus* range) (table 4.2 and fig. 4.2). The mean value of specimen NMR90 (144.37 mm) also falls just outside (below) the *C. l. lupus* sample range. For *c-b* the specimen range of NMR90, as well as its mean value, fall entirely within the sample range of *C. l. lupus*, although in the lower part. The specimen range of NMR90 falls well within the (fossil part of the) sample range of *C. l. familiaris* for both *a-b* and *c-b* (fig. VII.1). For *a-b* NMR90 falls entirely within the *Cuon alpinus* sample range, although in the higher part, but for *c-b* the specimen range only slightly overlaps with the *Cuon alpinus* sample range: the lower value of the range of NMR90 overlaps with 0.68 mm with the upper part of the *Cuon alpinus* sample range and the remaining 3.43 mm of the NMR90 specimen range falls outside (above) the *Cuon alpinus* range. The specimen range of NMR90 falls entirely outside (below) the population range of *C. l. lupus* and also entirely outside (above) the population range of *Cuon alpinus*, but well within the range of *C. l. familiaris* for *a-b* (table 4.2 and fig. 4.2). For *c-b* the specimen range of NMR90 falls entirely outside (above) the population range of *Cuon alpinus*, entirely within the *C. l. familiaris* range and overlaps slightly (1.36 mm) with the *C. l. lupus* population range, although most of the specimen range of NMR90 (2.75 mm) falls outside (below) the *C. l. lupus* range. The mean value of NMR90 (144.37 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 9.19 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (15.90 mm) and least similar to *C. l. lupus* (27.4 mm) for *a-b* (appendix XIII). Values are comparable for *c-b*. (The comparisons of the distances between means are relative: what is a large difference for one parameter is very small for the next, depending on the scales of the parameters.) Specimen NMR90 plots exactly on the *C. l. familiaris* trend line and is positioned above all *Cuon alpinus* specimens in fig. VIII.1 (for a fixed value of *a-b* NMR90 has a slightly higher value for *c-b* than *Cuon alpinus*).

**Table 4.2: Comparison of the specimen ranges of the fossil North Sea specimens with the sample and population ranges of the comparative material for parameters 'Length mandible' a-b (left) and c-b (right) (in mm).** Sample and population ranges of the comparative material are as given in table 4.1. Specimen ranges were calculated subtracting the margin or error for the specific parameter of and adding it to the mean value of the fossil specimen as given in appendix XIII (table 2.1 and appendix XIII). Specimen ranges of specimens 534 and 2329, specimens 1683, 2196 and 2620 and specimens 2103 and 3219 are identical (see corresponding paragraphs).

Canidae material		Length mandible a-b				Length mandible c-b			
		- Sample range +		- Population range +		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	145	200	147	197	143	200	146	198
	<i>C. l. familiaris</i>	102	173	98,2	172	103	178	99,6	173
	<i>Cuon alpinus</i>	108,25	149,32	113,92	143,01	106,22	143,93	112,58	140,01
Fossil North Sea	534, 2329	179	200	-	-	178	200	-	-
	667	143,64	145,60	-	-	143,25	145,21	-	-
	1683, 2196, 2620	198	200	-	-	198	200	-	-
	2103, 3219	144	162	-	-	143	161	-	-
	2104	140,82	142,78	-	-	142,78	144,74	-	-
	3293	179	181	-	-	178	180	-	-
	NMR89	159	161	-	-	160	162	-	-
	NMR90	143,13	145,60	-	-	143,25	147,36	-	-



**Figure 4.2: Scatter plot of parameters 'Length mandible' a-b vs. c-b for the fossil North Sea specimens and the comparative material (in mm).** Data points of the fossil North Sea specimens are given as the average value of its specimen range instead of the range itself, to not further complicate the figure with more minima and maxima (as explained in 2.2.3). These mean values can be found in appendix XIII. In the description of the results the specimen ranges (as given in table 4.2) will of course be taken into account. Legend, see fig. 4.1.

#### 4.1.2 Alveolar lengths $P_1$ - $M_2$ and $P_4$ - $M_2$

Alveolar lengths include the length of the tooth row and diastemata (if present, fig. III.2). In larger mandibles teeth can be placed at a larger distance from each other and there is more space for diastemata. Smaller mandibles have less space for all the teeth to fit in and consequently will have their teeth spaced more closely and possess less diastemata. Alveolar lengths can thus be used as indicator of mandible length: the smaller the alveolar length, the smaller the mandible probably was.

#### 4.1.2.1 Results comparative material

For all values see both table 4.3 and fig. 4.3 unless stated otherwise.

**x** For both parameters  $P_1-M_2$  and  $P_4-M_2$  *C. l. lupus* has on average the largest alveolar length (with 85.92 mm for  $P_1-M_2$  and 52.25 mm for  $P_4-M_2$ ), as also can be seen from its position in the upper part of fig. 4.3. *C. l. familiaris* and *Cuon alpinus* have significantly smaller alveolar lengths (*C. l. familiaris* with 68.01 mm for  $P_1-M_2$  and 41.03 mm for  $P_4-M_2$  and *Cuon alpinus* with 61.37 mm for  $P_1-M_2$  and 38.27 mm for  $P_4-M_2$ ) and plot closer together (in the lower part of fig. 4.3) than both *Canis* species.

**SD vs. n** For  $P_1-M_2$  *C. l. familiaris* shows the greatest variation in alveolar length (SD of 7.59 mm), while this species also has the greatest sample size (n 42). *C. l. lupus* on the other hand has a significantly smaller sample size than *C. l. familiaris*, but the standard deviation is almost as large (table 4.3). For parameter  $P_4-M_2$  the standard deviation of *C. l. lupus* is even larger than that of *C. l. familiaris*, while also for this parameter the sample size of *C. l. lupus* is much smaller. This is also evident from fig. 4.3: *C. l. familiaris* and *Cuon alpinus* data points lie more or less on a line, while the data points of *C. l. lupus* show much more scatter (S shape). *Cuon alpinus* has a smaller sample size than *C. l. familiaris*, but proportionally an even smaller standard deviation for both parameters.

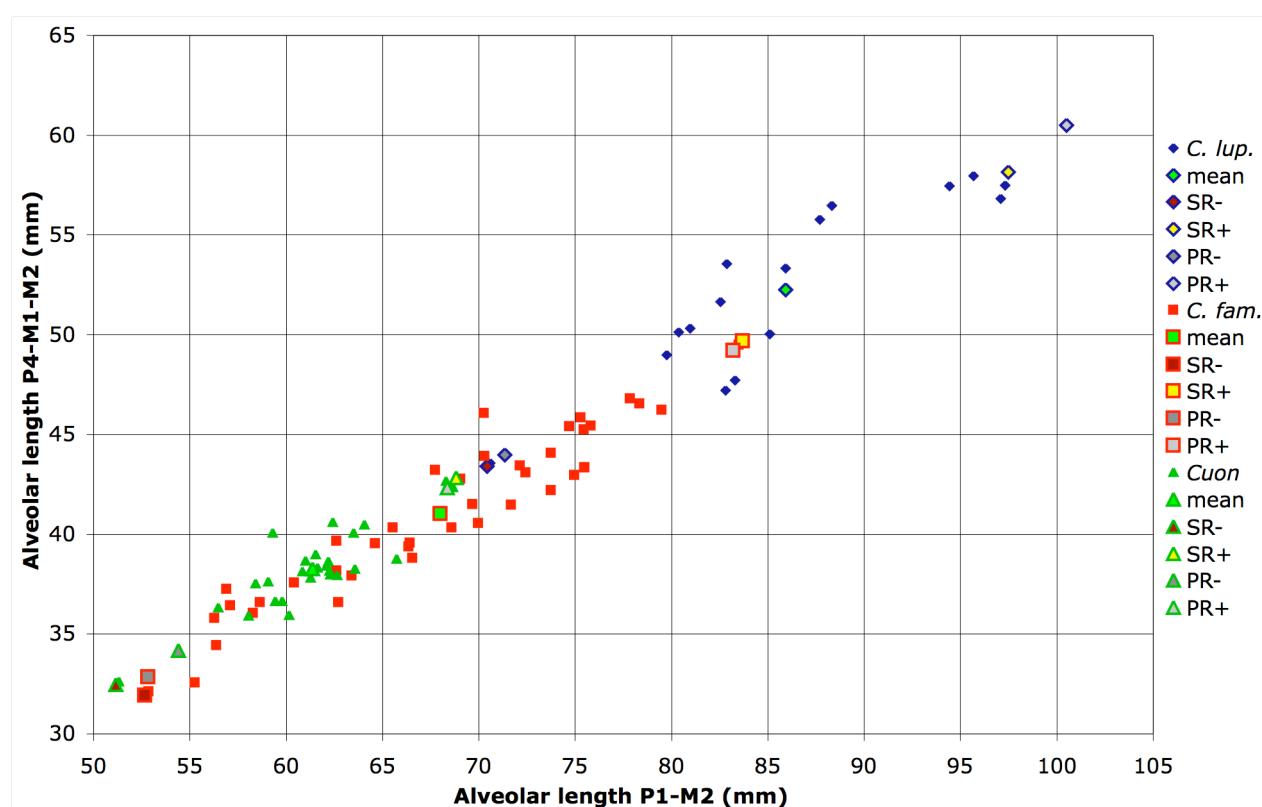
**Sample ranges** *Cuon alpinus* and *C. l. lupus* ranges are nicely separated for both parameters (by 1.59 mm for  $P_1-M_2$  and by 0.55 mm for  $P_4-M_2$ , also see the *Cuon alpinus* SR+ and *C. l. lupus* SR- data points in fig. 4.3), where *Cuon alpinus* plots in the lower part of the graph and *C. l. lupus* in the upper part. The *C. l. familiaris* sample range is large and plots from the lower part of fig. 4.3 well within the *C. l. lupus* range (but does not reach the *C. l. lupus* mean) overlapping significantly with both the *Cuon alpinus* and *C. l. lupus* sample ranges. Also for these parameters a distinction can be made within the *C. l. familiaris* group, separating the fossil specimens from the Netherlands from the recent specimens from Suriname. The recent specimens are distributed over the entire *C. l. familiaris* range, while the fossil specimens form a smaller data cloud in the upper part of fig. VII.2. The data points of *C. l. lupus* are not very evenly distributed along its range: almost all specimens plot in the upper part of fig. 4.3 (having a value above 79 mm for  $P_1-M_2$  and 47 mm for  $P_4-M_2$ ). Only one specimen, *lupus-m*, plots below these values and is separated from the rest by quite a distance (9 mm for  $P_1-M_2$ ). The *C. l. familiaris* range has a similar density of data points over its entire range and most *Cuon alpinus* data points are clustered around its mean (with specimen 20551 deviating the most from this cluster and being the *Cuon alpinus* with the smallest alveolar length). In these descriptions of the distribution of the specimens over their range the values of the standard deviation can also be seen: the bell-shaped curves of *Canis* are broad (large standard deviation), while that of *Cuon alpinus* is small (small standard deviation).

**Population ranges** Also for the population ranges the *Cuon alpinus* and *C. l. lupus* data clouds do not overlap (they are separated by 2.98 mm for  $P_1-M_2$  and by 1.66 mm for  $P_4-M_2$ ) (table 4.3). The *C. l. familiaris* range still shows great overlap with these both species: the *C. l. familiaris* PR- data point has an even lower value than the *Cuon alpinus* PR- data point and the *C. l. familiaris* PR+ plots well within the *C. l. lupus* data cloud (fig. 4.3).

**Trend lines** All three comparative species show less variation (lower standard deviations) in parameter  $P_4-M_2$  than in  $P_1-M_2$  (which can also be seen from the ranges of the x- and y-axes of fig. 4.3). Although for these parameters there is more variation and scatter in data points than for both 'Length mandible' parameters, the specimens of the three comparative species still follow more or less a linear trend in fig. VIII.2 and are well comparable. Trend lines of both *Canis* specimens are dissimilar: many *C. l. lupus* specimens have a relatively greater  $P_4-M_2$  length than  $P_1-M_2$  length compared to *C. l. familiaris* specimens. The *Cuon alpinus* trend line lies in between the *Canis* trend lines. There are no specimens that deviate extremely from these trend lines.

**Table 4.3: Statistics of the parameters 'Alveolar length' P<sub>1</sub>-M<sub>2</sub> (left) and P<sub>4</sub>-M<sub>2</sub> (right) of the comparative material (in mm). Legend: see table 4.1.**

Statistics	Alveolar length P <sub>1</sub> -M <sub>2</sub>			Alveolar length P <sub>4</sub> -M <sub>2</sub>		
	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>
Sample size (n)	16	42	26	18	42	27
Sample mean (x)	85,92	68,01	61,37	52,25	41,03	38,27
Standard deviation (SD)	7,29	7,59	3,49	4,13	4,09	2,04
Minimum (MIN)	70,60	52,85	51,32	43,58	32,12	32,64
Maximum (MAX)	97,31	83,50	68,65	57,96	49,51	42,67
Sample range MIN	70,42	52,67	51,14	43,40	31,94	32,46
Sample range MAX	97,49	83,68	68,83	58,14	49,69	42,85
Population range MIN	71,34	52,82	54,39	44,00	32,85	34,19
Population range MAX	100,5	83,19	68,36	60,51	49,21	42,34



**Figure 4.3: Scatter plot of parameters 'Alveolar length' P<sub>1</sub>-M<sub>2</sub> vs. P<sub>4</sub>-M<sub>2</sub> for the comparative material (in mm). Legend, see table 4.1.**

#### 4.1.2.2 Results fossil North Sea material

All alveolar lengths are measured directly on the fossil North Sea specimens, thus qualitative comparison of the specimens with the comparative material was not needed. In this section no qualitative descriptions of the fossil North Sea specimens are given.

##### Specimens 534 and 535

For specimen 534 and 535 parameters 'Alveolar length' P<sub>1</sub>-M<sub>2</sub> and P<sub>4</sub>-M<sub>2</sub> could not be measured or estimated by comparison, because a large (anterior) part of the hemimandible is absent (appendix I). No data is available.

### Specimen 667

The specimen range of 667 falls entirely outside (below) the sample and population ranges of *C. l. lupus* for both parameters and entirely within the sample and population ranges of *C. l. familiaris* (fossil part) and *Cuon alpinus* (table 4.4 and fig. 4.4). Specimen 667 is clearly smaller than all *C. l. lupus* material. For parameter  $P_1-M_2$  the mean value of 667 (66.14 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 1.87 mm between the two mean values) and also very similar to the *Cuon alpinus* mean (4.77 mm, appendix XIII). In fig. 4.4 specimen 667 plots in between those two means. Specimen 667 is very dissimilar to the average *C. l. lupus* specimen (with 19.78 mm). For parameter  $P_4-M_2$  this trend is similar, with the mean of 667 (39.31 mm) plotting in between the means of *Cuon alpinus* and *C. l. familiaris* and being most dissimilar to *C. l. lupus* (with a distance of 12.94 mm between the two mean values), although for this parameter 667 is most similar to *Cuon alpinus* (with 1.04 mm) instead of *C. l. familiaris* (1.72 mm). Specimen 667 lies closest to the trend line of *C. l. familiaris*, far away from *C. l. lupus* specimens, but does not plot outside the *Cuon alpinus* data cloud and is not positioned significantly far away from *Cuon alpinus* data points (fig. VIII.2).

### Specimen 1683

The specimen range of 1683 falls entirely within the (upper part of the) *C. l. lupus* sample and population range and entirely outside (far above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* (table 4.4 and fig. 4.4). Specimen 1683 has much larger alveolar lengths than *C. l. familiaris* and *Cuon alpinus* specimens. As is already very clear from fig. 4.4, specimen 1683 is most similar to *C. l. lupus*. The mean of 1683 lies closest to the average *C. l. lupus* specimen (with a distance of 10.14 mm between the two mean values for  $P_1-M_2$ ) and significantly further away from the average *C. l. familiaris* (28.05 mm) and *Cuon alpinus* specimen (34.69 mm, appendix XIII). This trend is the same for parameter  $P_4-M_2$ . Specimen 1683 plots very close to the *C. l. lupus* trend line, far above the *C. l. familiaris* and *Cuon alpinus* data clouds (fig. VIII.2).

### Specimen 2103

The specimen range of 2103 falls entirely within the *Canis* sample and population ranges and entirely outside (above) the *Cuon alpinus* sample and population ranges for parameter  $P_1-M_2$  (table 4.4 and fig. 4.4). Specimen 2103 falls entirely outside (below) the *C. l. lupus* sample and population ranges for parameter  $P_4-M_2$ . Specimen 2103 falls within the *Cuon alpinus* sample range for  $P_4-M_2$  (although in the upper part), but entirely outside (above) corresponding population range and entirely within the *C. l. familiaris* sample and population ranges (fossil part) for this parameter (fig. VII.2). The mean value of specimen 2103 is most similar to the average *C. l. familiaris* specimen (with a distance of 5.39 mm between the two mean values for  $P_1-M_2$  and a distance of 1.51 mm between the two mean values for  $P_4-M_2$ , appendix XIII). Specimen 2103 is less similar to the average *Cuon alpinus* specimen (with respectively 12.03 mm and 4.27 mm for parameters  $P_1-M_2$  and  $P_4-M_2$ ) and least similar to the average *C. l. lupus* specimen (with respectively 12.52 mm and 9.71 mm for parameters  $P_1-M_2$  and  $P_4-M_2$ ). Specimen 2103 plots closest to the trend line of *C. l. familiaris* and has a relatively small  $P_4-M_2$  length compared to its  $P_1-M_2$  length in comparison to *Cuon alpinus* and *C. l. lupus* data points (fig. VIII.2).

### Specimen 2104

The specimen range of 2104 falls entirely within the *C. l. lupus* sample range, but only partially within corresponding population range for parameter  $P_1-M_2$  (overlap is 0.27 mm, while 0.09 mm of the specimen range falls outside the population range, table 4.4 and fig. 4.4). Specimen 2104 falls entirely outside (below) the *C. l. lupus* sample and population ranges for  $P_4-M_2$  and entirely outside (above) the *Cuon alpinus* sample and population ranges for  $P_1-M_2$ . This fossil specimen falls in all other sample and population ranges (and within the fossil part of the *C. l. familiaris* ranges, fig. VII.2). The mean value of specimen 2104 is most similar to the average *C. l. familiaris* specimen (with a distance of 3.42 mm between the two mean values for  $P_1-M_2$  and a distance of 0.04 mm between the two mean values for  $P_4-M_2$ , appendix XIII). Specimen 2104 is less similar to the average *Cuon alpinus* specimen (with respectively 10.06 mm and 2.80 mm for parameters  $P_1-M_2$  and  $P_4-M_2$ ) and least similar to the average *C. l. lupus* specimen (with respectively 14.49 mm and 11.18 mm for parameters  $P_1-M_2$  and  $P_4-M_2$ ). The position of specimen 2104 in fig. VIII.2 is similar to that of 2103: it plots closest to the trend line of *C. l. familiaris* and has a relatively small  $P_4-M_2$  length compared to its  $P_1-M_2$  length in comparison to *Cuon alpinus* and *C. l. lupus* data points.

### Specimen 2196

Specimen 2196 has very large alveolar lengths compared to *Cuon alpinus* and *C. l. familiaris* and falls outside (above) the sample and population ranges of these (sub)species for both parameters (table 4.4 and fig. 4.4). Specimen 2196 plots entirely within the sample range of *C. l. lupus* for parameter  $P_1-M_2$ , just above the *C. l. lupus* sample range for  $P_4-M_2$  and falls entirely within the (upper part of the) population ranges of *C. l. lupus* for both parameters. As is already obvious from fig. 4.4, specimen 2196 is most similar to the average *C. l. lupus* specimen (with a distance of 8.64 mm between the two mean values for  $P_1-M_2$ ) and very

dissimilar to *C. I. familiaris* and *Cuon alpinus* specimens (with 26.55 and 33.19 mm respectively, appendix XIII). This trend is the same for parameter  $P_4-M_2$ . Specimen 2104 plots closest to the *C. I. lupus* trend line, far away from the *C. I. familiaris* and *Cuon alpinus* data clouds (fig. VIII.2).

#### **Specimen 2329**

Specimen 2329 falls entirely within the *C. I. lupus* sample and population ranges and entirely outside (above) the *C. I. familiaris* and *Cuon alpinus* sample and population ranges for both parameters (table 4.4 and fig. 4.4). As is already obvious from fig. 4.4, specimen 2329 is most similar to the average *C. I. lupus* specimen (with a distance of 2.45 mm between the two mean values for  $P_1-M_2$ ) and very dissimilar to *C. I. familiaris* and *Cuon alpinus* specimens (with 20.36 and 27.00 mm respectively, appendix XIII). This trend is the same for parameter  $P_4-M_2$ . Specimen 2329 plots closest to the *C. I. lupus* trend line, far away from the *C. I. familiaris* and *Cuon alpinus* data clouds (fig. VIII.2).

#### **Specimen 2620**

Specimen 2620 falls entirely within the *C. I. lupus* sample range for parameter  $P_4-M_2$ , outside (above) the *C. I. lupus* sample range for parameter  $P_1-M_2$  and entirely within the *C. I. lupus* population range for both parameters (table 4.4 and fig. 4.4). Specimen 2620 falls far outside (above) the sample and population ranges of *C. I. familiaris* and *Cuon alpinus*. As is already obvious from fig. 4.4, specimen 2620 is most similar to the average *C. I. lupus* specimen (with a distance of 12.33 mm between the two mean values for  $P_1-M_2$ ) and very dissimilar to *C. I. familiaris* and *Cuon alpinus* specimens (with 30.24 and 26.88 mm respectively, appendix XIII). This trend is the same for parameter  $P_4-M_2$ . Specimen 2620 plots closest to the *C. I. lupus* trend line far away from the *C. I. familiaris* and *Cuon alpinus* data clouds (fig. VIII.2).

#### **Specimen 3219**

Specimen 3219 falls entirely within the sample and population ranges of both *Canis* species (and within the fossil part of the *C. I. familiaris* sample range) and entirely outside (above) the *Cuon alpinus* sample and population ranges for both parameters (table 4.4 and fig. 4.4). The mean value of specimen 3219 is most similar to the average *C. I. familiaris* specimen (with a distance of 4.67 mm between the two mean values for  $P_1-M_2$ ) and more dissimilar to *Cuon alpinus* and *C. I. lupus* (with a distance of respectively 11.31 and 13.24 mm, appendix XIII). This trend is similar for parameter  $P_4-M_2$ . Specimen 3219 lies in between the trend lines of both *Canis* specimens, above the *Cuon alpinus* data cloud. It plots only slightly closer to the *C. I. lupus* trend line, but not outside either of both *Canis* data clouds (fig. VIII.2).

#### **Specimen 3293**

Specimen 3293 falls entirely within the sample and population ranges of *C. I. lupus* and entirely outside (above) the *C. I. familiaris* and *Cuon alpinus* sample and population ranges for both parameters (table 4.4 and fig. 4.4). The mean value of specimen 3293 is most similar to the average *C. I. lupus* specimen (with a distance of 3.58 mm between the two mean values for  $P_1-M_2$ ) and much more dissimilar to the average *C. I. familiaris* and *Cuon alpinus* specimens (with 21.49 and 28.13 mm, appendix XIII). This trend is similar for parameter  $P_4-M_2$ . Specimen 3293 plots very close to the *C. I. lupus* trend line, far above the *C. I. familiaris* and *Cuon alpinus* data clouds (fig. VIII.2).

#### **Specimen NMR89**

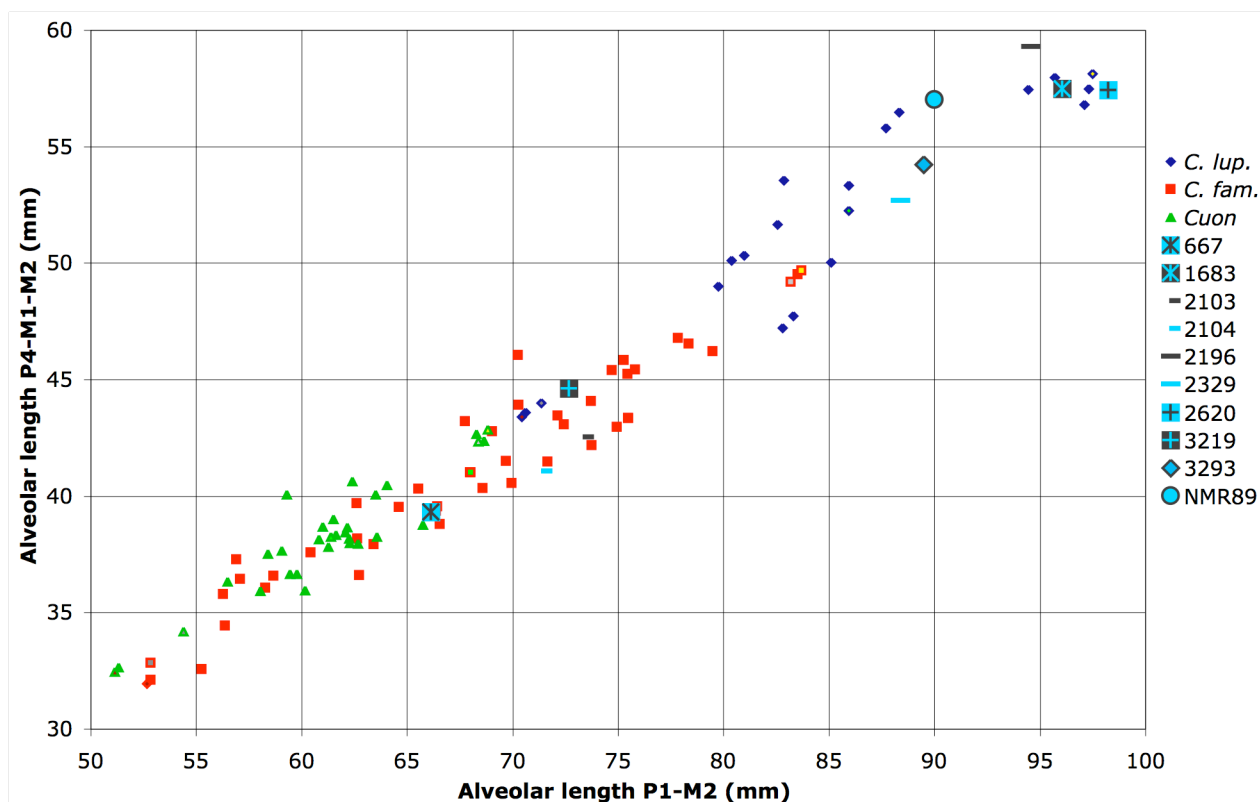
The specimen range of NMR89 falls entirely within the sample and population ranges of *C. I. lupus* and entirely outside (above) the sample and population ranges of *C. I. familiaris* and *Cuon alpinus* for both parameters (table 4.4 and fig. 4.4). The mean value of NMR89 is most similar to the average *C. I. lupus* specimen (with a distance of 4.08 mm between the two mean values for  $P_1-M_2$ ) and much more dissimilar to the average *C. I. familiaris* and *Cuon alpinus* specimens (with 21.99 and 28.63 mm, appendix XIII). This trend is similar for parameter  $P_4-M_2$ . As is obvious from fig. VIII.2 NMR89 plots closest to the *C. I. lupus* trend line in the upper part of the plot, far above the *C. I. familiaris* and *Cuon alpinus* data clouds.

#### **Specimen NMR90**

For parameter  $P_1-M_2$  there is no data available for NMR90, because a large anterior part of the hemimandible misses. Only parameter  $P_4-M_2$  could be measured and as a result NMR90 could not be plotted in figures 4.4 and VIII.2. The specimen range of NMR90 falls just outside (below) the *C. I. lupus* sample range (with only 0.12 mm between the two ranges) and also slightly outside (above) the *Cuon alpinus* range (with only 0.07 mm between the two ranges) and also entirely outside the population ranges of *C. I. lupus* and *Cuon alpinus* (table 4.4). NMR90 falls entirely within the *C. I. familiaris* sample and population ranges (fossil part). The mean value of NMR90 is most similar to the average *C. I. familiaris* specimen (with a distance of 2.07 mm between the two mean values for  $P_1-M_2$ ), less similar to the average *Cuon alpinus* specimen (with 4.83 mm) and most dissimilar to the average *C. I. lupus* specimen (with 9.15 mm, appendix XIII).

**Table 4.4: Comparison of the specimen ranges of the fossil North Sea specimens with the sample and population ranges of the comparative material for parameters ‘Alveolar length’ P<sub>1</sub>-M<sub>2</sub> (left) and P<sub>4</sub>-M<sub>2</sub> (right) (in mm). Sample and population ranges of the comparative material are as given in table 4.3. Specimen ranges were calculated as explained in table 4.2.**

Canidae material		Alveolar length P <sub>1</sub> -M <sub>2</sub>				Alveolar length P <sub>4</sub> -M <sub>2</sub>			
		- Sample range +		- Population range +		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	70,42	97,49	71,34	100,5	43,40	58,14	44,00	60,51
	<i>C. l. familiaris</i>	52,67	83,68	52,82	83,19	31,94	49,69	32,85	49,21
	<i>Cuon alpinus</i>	51,14	68,83	54,39	68,36	32,46	42,85	34,19	42,34
Fossil North Sea	667	65,96	66,32	-	-	39,13	39,49	-	-
	1683	95,88	96,24	-	-	57,3	57,66	-	-
	2103	73,22	73,58	-	-	42,36	42,72	-	-
	2104	71,25	71,61	-	-	40,89	41,25	-	-
	2196	94,38	94,74	-	-	59,12	59,48	-	-
	2329	88,19	88,55	-	-	52,5	52,86	-	-
	2620	98,07	98,43	-	-	57,25	57,61	-	-
	3219	72,50	72,86	-	-	44,43	44,79	-	-
	3293	89,32	89,68	-	-	54,06	54,42	-	-
	NMR89	89,82	90,18	-	-	56,84	57,20	-	-
	NMR90	-	-	-	-	42,92	43,28	-	-



**Figure 4.4: Scatter plot of parameters ‘Alveolar length’ P<sub>1</sub>-M<sub>2</sub> vs. P<sub>4</sub>-M<sub>2</sub> for the fossil North Sea specimens and the comparative material (in mm). Legend, see tables 4.1 and 4.2.**

#### Values from literature

The parameter ‘Alveolar length P<sub>1</sub>-M<sub>2</sub>’ is the first of the six parameters for which values of a comparative species were found in literature that fall outside the sample and/or population ranges that were already calculated with the original comparative dataset (appendix IX). The other five parameters for which values were found in literature are: Alveolar length M<sub>1</sub>-M<sub>2</sub>, Mandible height *h-h'* under M<sub>1</sub>, Length of tooth M<sub>1</sub> and the Breadth of teeth M<sub>1</sub> and M<sub>2</sub>. Results of the values from literature for each of these parameters will be discussed at the end of each corresponding paragraph. For all these six parameters the only values from literature that fell outside the original ranges were from *Cuon alpinus* specimens and all were larger than the originally calculated maximum for that parameter. The new comparative *Cuon alpinus* dataset including the



values from literature is analyzed separately and does not replace the original comparative *Cuon alpinus* dataset, because it was not explained in the literature how the parameters were taken exactly. A slightly different measuring method can be the cause that the *Cuon alpinus* values from the literature fall outside (above) the ranges obtained with the original dataset. This new comparative dataset is only used as additional comparison. For the parameter 'Alveolar length P<sub>1</sub>-M<sub>2</sub>' values of six *Cuon alpinus* specimens were found in Pérez Ripoll et al. (2010) (appendix IX). These values were added to the comparative dataset (which resulted in a sample size of 32 instead of 26) and new statistics were calculated (appendix IX). The fossil North Sea specimens were compared to the new ranges and results will be discussed briefly in this paragraph (appendix XII).

For specimens 667, 1683, 2196, 2329, 2620, 3293 and NMR89 the results obtained by the comparison of the specimen ranges with the new comparative ranges confirm previous results: specimen 667 falls entirely inside the sample and population ranges of *Cuon alpinus* and specimens 1683, 2196, 2329, 2620, 3293 and NMR89 fall entirely outside the *Cuon alpinus* sample and population ranges (table 4.4 and appendix IX). For specimens 2103, 2104 and 3219 the specimen ranges fall entirely inside the new *Cuon alpinus* sample and population ranges, whereas they fell entirely outside these both ranges compared to the original *Cuon alpinus* dataset.

### 4.1.3 Alveolar length M<sub>1</sub>-M<sub>2</sub>

Three alveolar lengths were measured: P<sub>1</sub>-M<sub>2</sub>, P<sub>4</sub>-M<sub>2</sub> (fig. III.2) and M<sub>1</sub>-M<sub>2</sub>. Comparison of the sample and population ranges of these three parameters with the specimen ranges of the fossil North Sea material revealed that the combination of the first two parameters gave the most conclusive evidence for the identity of the fossil specimens i.e. based on alveolar lengths P<sub>1</sub>-M<sub>2</sub> and P<sub>4</sub>-M<sub>2</sub> the identity of 9 of the 13 fossil North Sea specimens could be determined, while for any other combination of parameters this amount was less. Moreover, the combination of these two parameters in one plot visualized best the comparative data clouds and fossil specimens positions, which is the primary goal of the figures. Thus it was decided that these two parameters would be analyzed together (as was done in the previous paragraph). Then only 'Alveolar length' M<sub>1</sub>-M<sub>2</sub> remains, which is a very similar parameter to P<sub>4</sub>-M<sub>2</sub> and which gives exactly the same or less information about the identities of the fossil North Sea specimens. For example, specimen NMR90, which could be determined as a *C. l. familiaris* specimen based on parameter P<sub>4</sub>-M<sub>2</sub> (see Chapter 5), can only be determined as *Canis* specimen for parameter M<sub>1</sub>-M<sub>2</sub>, which is less conclusive (appendix XII). For all fossil specimens (except one) the conclusions based on parameter M<sub>1</sub>-M<sub>2</sub> thus only confirm those already obtained by parameters P<sub>1</sub>-M<sub>2</sub> and P<sub>4</sub>-M<sub>2</sub> or are less conclusive (as was the case for NMR90). Therefore parameter M<sub>1</sub>-M<sub>2</sub> will not be analyzed into detail (statistics of the comparative material and values of all fossil specimen can be found in appendices X and XIII, no plots are made). Specimen 535 is the only fossil North Sea specimen for which parameter M<sub>1</sub>-M<sub>2</sub> gives new information about its identity, therefore only the results of this specimen will be presented here.

#### Specimen 535

The specimen range of 535 falls entirely within the sample and population ranges of *C. l. lupus* and entirely outside (above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* for parameter M<sub>1</sub>-M<sub>2</sub> (table 4.5). The mean value of 535 is most similar to the average *C. l. lupus* specimen (with a distance of 1.82 mm between the two mean values) and less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 9.83 and 11.55 mm respectively, appendix XIII).

**Table 4.5: Comparison of the specimen range of fossil North Sea specimen 535 with the sample and population ranges of the comparative material for parameter 'Alveolar length' M<sub>1</sub>-M<sub>2</sub> (in mm).** Specimen ranges were calculated as explained in table 4.2 and are given for all fossil North Sea specimen in table X.1.

Canidae material		Alveolar length M <sub>1</sub> -M <sub>2</sub>			
		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	32,11	44,70	32,42	43,43
	<i>C. l. familiaris</i>	24,09	38,25	24,30	35,52
	<i>Cuon alpinus</i>	23,33	31,55	25,20	31,19
NS	535	39,56	39,92	-	-

### Values from literature

'Alveolar length  $M_1$ - $M_2$ ' is the second parameter for which (six) values of comparative *Cuon alpinus* specimens were found in literature (Pérez Ripoll et al., 2010) that fall outside (above) the sample and/or population ranges that were already calculated based on the original comparative dataset. These six values were added to the comparative dataset (which resulted in a sample size of 33 instead of 27) and new statistics were calculated (appendix IX). The fossil North Sea specimens were compared to the new ranges and this resulted in the following results (see also appendix XII):

For specimens 535, 667, 1683, 2104, 2196, 2329, 2620, 3293 and NMR89 the results obtained by the comparison to the new comparative ranges confirm previous results: specimens 667 and 2104 fall entirely inside the *Cuon alpinus* sample and population ranges and specimens 535, 1683, 2196, 2329, 2620, 3293 and NMR89 fall entirely outside the *Cuon alpinus* sample and population ranges (compare table X.1 and IX.2). For the last three fossil North Sea specimens results are different. Specimen 2103 originally fell partly outside the *Cuon alpinus* sample range and entirely outside the corresponding population range, but falls entirely within the new *Cuon alpinus* sample and population ranges. Specimen NMR90 originally fell outside the *Cuon alpinus* sample and population ranges, but falls entirely within both new *Cuon alpinus* ranges. Specimen 3219 originally fell entirely outside both *Cuon alpinus* ranges and still falls outside (above) the new *Cuon alpinus* population range, but falls within the new *Cuon alpinus* sample range.

## 4.1.4 Mandibular diastema length

Relative shortness of the mandibles of *Cuon alpinus* can be observed among other things by absence of the mandibular diastemata (García and Arsuaga, 1998) and reduced upper diastemata (García and Arsuaga, 1998 and Pérez Ripoll et al., 2010). But a quick initial look into the comparative *Cuon alpinus* dataset, revealed that almost all *Cuon alpinus* specimens *did* have mandibular diastemata between their canines and premolars and that more than half of the specimens also had diastemata between their premolars. This leads to the hypothesis, that not only the absence of diastemata is an indication for the relative shortness of the mandibles of *Cuons*, but that, when diastemata are present in *Cuon alpinus*, they will be reduced in size compared to *Canis*. (as observed by Pérez Ripoll et al., 2010). To test this hypothesis diastemata between  $C_1$  and  $P_1$  were measured quantitatively. Additionally, the presence, absence and relative size of other diastemata (between premolars) were recorded, as discussed below.

### 4.1.4.1 Diastema length C- $P_1$

#### 4.1.4.1a Results comparative material

For all values see both table 4.6 and fig. 4.5 unless stated otherwise.

**x** *C. l. lupus* has on average the largest diastema length between its C and  $P_1$  (fig. III.2) (with 6.75 mm), followed closely by *C. l. familiaris* (with 5.63 mm), which is obvious from fig. 4.5. But *Cuon alpinus* specimens also possess diastemata between their canines and first premolars, which, with an average length of 3.10 mm, are about half the length of diastemata of *Canis* specimens (table 4.6). For this parameter averages of both *Canis* species lie closer together than the *C. l. familiaris* and *Cuon alpinus* means.

**SD vs. n** *C. l. lupus* shows the greatest variation in diastema length (SD of 1.85 mm), but has the smallest sample size. *C. l. familiaris* has a much larger sample size than *C. l. lupus*, but a smaller standard deviation (table 4.6). *Cuon alpinus* has again a sample size in between those of the *Canis* species, but the smallest standard deviation and thus the least variation in its dataset, although the difference with the *Canis* standard deviations is less than for previous parameters. Note that the reason that the *Cuon alpinus* sample size (n) is smaller than the entire dataset is that two *Cuon alpinus* specimens did not possess a C- $P_1$  diastema. But both *Canis* sample sizes are slightly smaller than their original samples size, because the C- $P_1$  diastema could not be measured and not because this diastema was absent in those specimens.

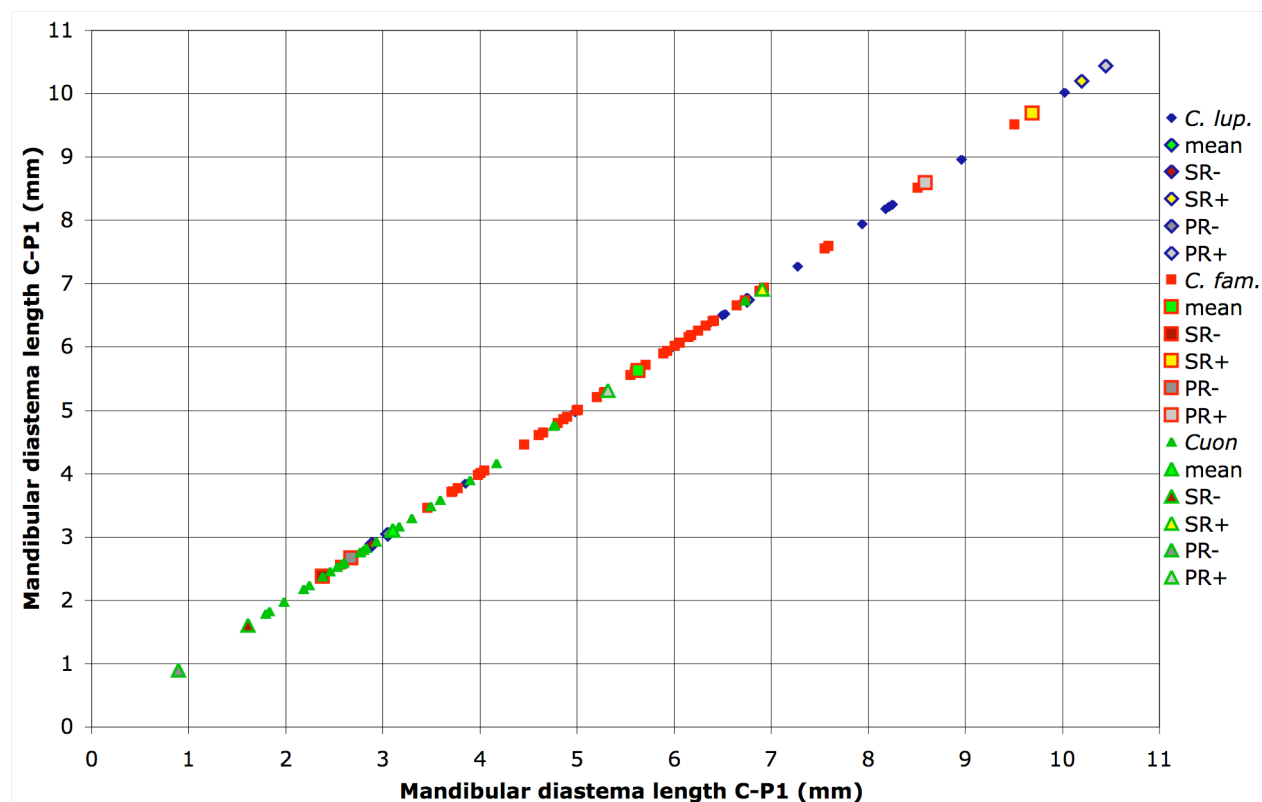
**Sample ranges** Although *Cuon alpinus* specimens form the lower most part of fig. 4.5 and *C. l. lupus* specimens the upper most part, all sample ranges overlap significantly with each other: the *Cuon alpinus* sample range maximum is even larger than the *C. l. lupus* mean and the *C. l. lupus* sample range minimum is smaller than the *Cuon alpinus* mean. The *C. l. familiaris* sample range is also large and plots from the lower part of fig. 4.5 far into the *C. l. lupus* range overlapping significantly with both the *Cuon alpinus* and *C. l. lupus* sample ranges. Also for this parameter a distinction can be made within the *C. l. familiaris* group, separating the fossil specimens from the Netherlands from the recent specimens from Suriname, although there is not much differences between the specimens of those two groups. The recent specimens are distributed over the entire *C. l. familiaris* range, while the fossil specimens form a slightly smaller data cloud in the upper part of fig. VII.3. The data points of the comparative species are quite very evenly distributed along their range: although the distance between specimens becomes slightly larger towards the upper parts of fig. 4.5, there are no specimens that deviate extremely from the rest of the group.

**Population ranges.** Also the population ranges overlap significantly: the minima of both *Canis* specimens plot below the *Cuon alpinus* mean and the *C. l. familiaris* maximum plots above the *C. l. lupus* mean (fig. 4.5). The *Cuon alpinus* maximum does not reach the *Canis* means, but does plot within both ranges.

**Trend lines** Since there is only one quantitatively measured diastema length, this parameter is plotted against itself and trend lines are not plotted.

**Table 4.6: Statistics of the parameter 'Mandibular diastema length' C-P<sub>1</sub> of the comparative material (in mm).** Legend: see table 4.1.

Statistics	Mandibular diastema length C-P <sub>1</sub>		
	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>
Sample size (n)	16	41	27
Sample mean (x)	6,75	5,63	3,10
Standard deviation (SD)	1,85	1,48	1,10
Minimum (MIN)	3,07	2,56	1,79
Maximum (MAX)	10,0	9,51	6,73
Sample range MIN	2,89	2,38	1,61
Sample range MAX	10,2	9,69	6,91
Population range MIN	3,05	2,67	0,89
Population range MAX	10,4	8,59	5,31



**Figure 4.5: Scatter plot of parameter 'Mandibular diastema length' C-P<sub>1</sub> vs. itself for the comparative material (in mm).** Legend, see table 4.1.

#### 4.1.4.1b Results fossil North Sea material

In this section no qualitative descriptions of the fossil North Sea specimens are given.

##### Specimens 534, 535, NMR89 and NMR90

The parameter 'Mandibular diastema length' C-P<sub>1</sub> could not be measured for these four fossil specimens, because a large (anterior) part of the hemimandible is absent (appendix I). No data is available.

**Specimen 667**

The specimen range of 667 falls entirely within the sample and population ranges of both *Canis* specimens (within the fossil part of the *C. l. familiaris* sample range) and entirely within the *Cuon alpinus* sample range (table 4.7 and fig. 4.6). Specimen 667 falls outside (above) the population range of *Cuon alpinus*. The mean value of specimen 667 for this parameter (5.78 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.15 mm between the two mean values), also quite similar to the average *C. l. lupus* specimen (with 0.97 mm) and more dissimilar to the average *Cuon alpinus* specimen (appendix XIII).

**Specimen 1683**

Specimen 1683 falls within the sample and population range of *C. l. lupus* and also inside the sample range of *C. l. familiaris*, but entirely outside (above) the population range of *C. l. familiaris* and the sample and population range of *Cuon alpinus* (table 4.7 and fig. 4.6). The mean value of specimen 1683 for this parameter (9.20 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 2.45 mm between the two mean values), less similar to the average *C. l. familiaris* specimen (with 3.57 mm) and most dissimilar to the average *Cuon alpinus* (with 6.10 mm) (appendix XIII).

**Specimen 2103**

Specimen 2103 falls entirely within the sample and population ranges of both *Canis* species (fossil part of the *C. l. familiaris* sample range) (table 4.7, fig. 4.6 and fig. VII.3). The specimen range of 2103 also falls entirely within the sample range of *Cuon alpinus*, but outside (above) its population range. The mean value of specimen 2103 for this parameter (6.33 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.42 mm between the two mean values), also quite similar to the average *C. l. familiaris* specimen (with 0.70 mm) and dissimilar to the average *Cuon alpinus* specimen (with 3.23 mm) (appendix XIII).

**Specimen 2104**

Specimen 2104 falls entirely inside the sample and population ranges of both *Canis* species (fossil part of the *C. l. familiaris* sample range, fig. VII.3) and entirely outside (above) the *Cuon alpinus* sample and population ranges (table 4.7 and fig. 4.6). The mean value of specimen 2104 for this parameter (7.20 mm) is also most similar to the average *C. l. lupus* specimen (with a distance of 0.45 mm between the two mean values), more dissimilar to the average *C. l. familiaris* specimen (with 1.57 mm) and most dissimilar to *Cuon alpinus* (with 4.10 mm) (appendix XIII).

**Specimen 2196**

Specimen 2196 plots very close to specimen 2104 in fig. 3.11 and consequently also has the same results: 2196 falls entirely inside the sample and population ranges of both *Canis* species and entirely outside (above) the *Cuon alpinus* sample and population ranges (table 4.7 and fig. 4.6). The mean value of specimen 2196 for this parameter (7.27 mm) is again most similar to the average *C. l. lupus* specimen (with a distance of 0.52 mm between the two mean values), less similar to the average *C. l. familiaris* specimen (with 1.64 mm) and most dissimilar to *Cuon alpinus* (with 4.17 mm) (appendix XIII).

**Specimen 2329**

Specimen 2329 also plot very close to previous two fossil North Sea specimens and also shows the same result: it falls entirely inside the sample and population ranges of both *Canis* species and entirely outside (above) the *Cuon alpinus* sample and population ranges (table 4.7 and fig. 4.6). The mean value of specimen 2329 for this parameter (7.94 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 1.19 mm between the two mean values), less similar to the average *C. l. familiaris* specimen (2.31 mm) and most dissimilar to *Cuon alpinus* (4.84 mm) (appendix XIII).

**Specimen 2620**

The specimen range of 2620 falls entirely within the sample and population ranges of *C. l. familiaris* and *C. l. lupus* (table 4.7 and fig. 4.6). This specimen also falls entirely within the *Cuon alpinus* specimen range, but entirely outside corresponding population range. The mean value of specimen 2620 for this parameter (6.50 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.25 mm between the two mean values), less similar to the average *C. l. familiaris* specimen (with 0.87 mm) and most dissimilar to the average *Cuon alpinus* specimen (3.40 mm) (appendix XIII).

**Specimen 3219**

The specimen range of 3219 falls entirely within the sample and population ranges of *C. l. familiaris* and *C. l. lupus* (table 4.7 and fig. 4.6). This specimen falls only partially within the *Cuon alpinus* specimen range (it overlaps with the upper part of this range), but entirely outside corresponding population range. The mean value of specimen 3219 for this parameter (7.00 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.25 mm between the two mean values), less similar to the average *C. l. familiaris*

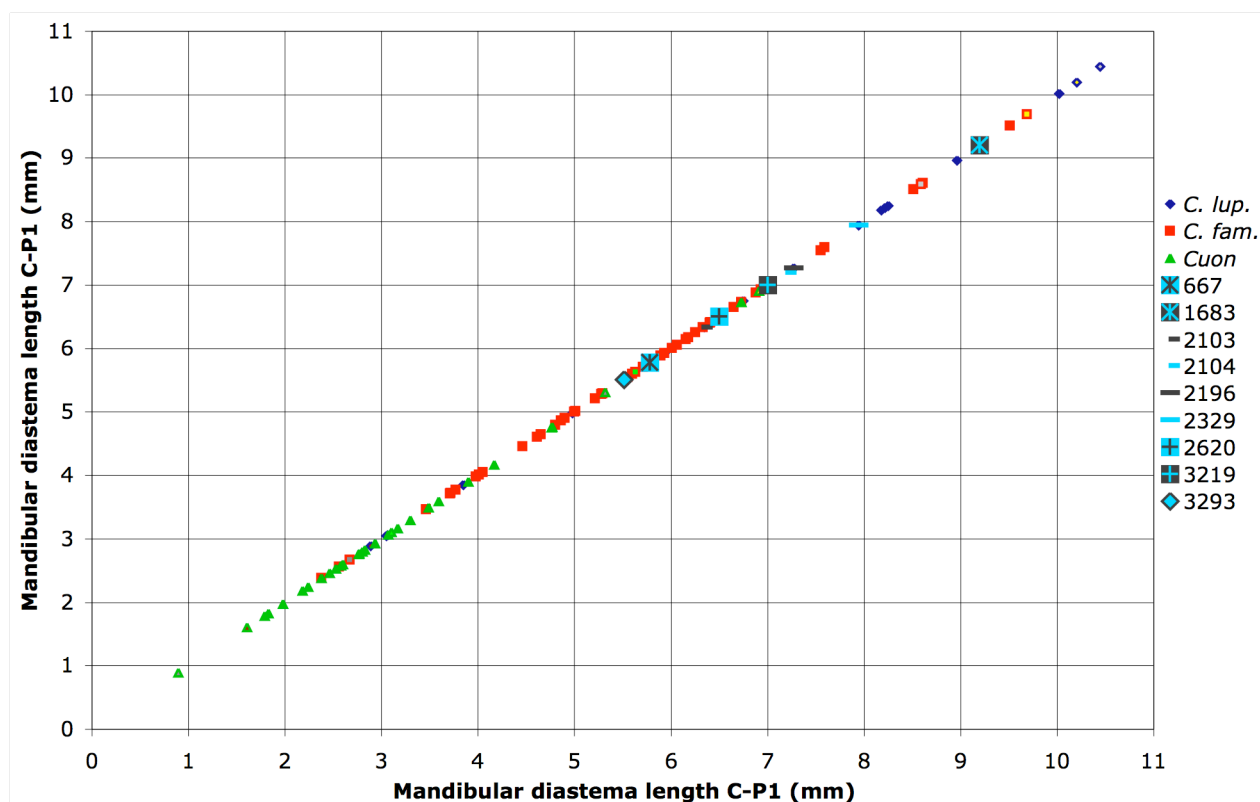
specimen (with 1.37 mm) and most dissimilar to the average *Cuon alpinus* specimen (3.90 mm) (appendix XIII).

### Specimen 3293

The specimen range of 3293 falls entirely within the sample and population ranges of *C. l. familiaris* and *C. l. lupus* (table 4.7 and fig. 4.6). This fossil specimen also falls within the sample range of *Cuon alpinus*, but just outside (above) the population range. The mean value of specimen 3293 for this parameter (5.51 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.12 mm between the two mean values), less similar to the average *C. l. lupus* specimen (with 1.24 mm) and dissimilar to the average *Cuon alpinus* specimen (2.41 mm) (appendix XIII).

**Table 4.7: Comparison of the specimen ranges of the fossil North Sea specimens with the sample and population ranges of the comparative material for parameter 'Mandibular diastema length' C-P<sub>1</sub> (in mm).** Sample and population ranges of the comparative material are as given in table 4.6. Specimen ranges were calculated as explained in table 4.2.

Canidae material		Mandibular diastema length C-P <sub>1</sub>			
		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	2,89	10,2	3,05	10,4
	<i>C. l. familiaris</i>	2,38	9,69	2,67	8,59
	<i>Cuon alpinus</i>	1,61	6,91	0,89	5,31
Fossil North Sea	667	5,60	5,96	-	-
	1683	9,02	9,38	-	-
	2103	6,15	6,51	-	-
	2104	7,02	7,38	-	-
	2196	7,09	7,45	-	-
	2329	7,76	8,12	-	-
	2620	6,32	6,68	-	-
	3219	6,82	7,18	-	-
	3293	5,33	5,69	-	-



**Figure 4.6: Scatter plot of parameter 'Mandibular diastema length' C-P<sub>1</sub> vs. itself for the fossil North Sea specimens and the comparative material (in mm).** Legend, see tables 4.1 and 4.2.

#### 4.1.4.2 Diastemata lengths P<sub>2</sub>-P<sub>3</sub> and/or P<sub>3</sub>-P<sub>4</sub>

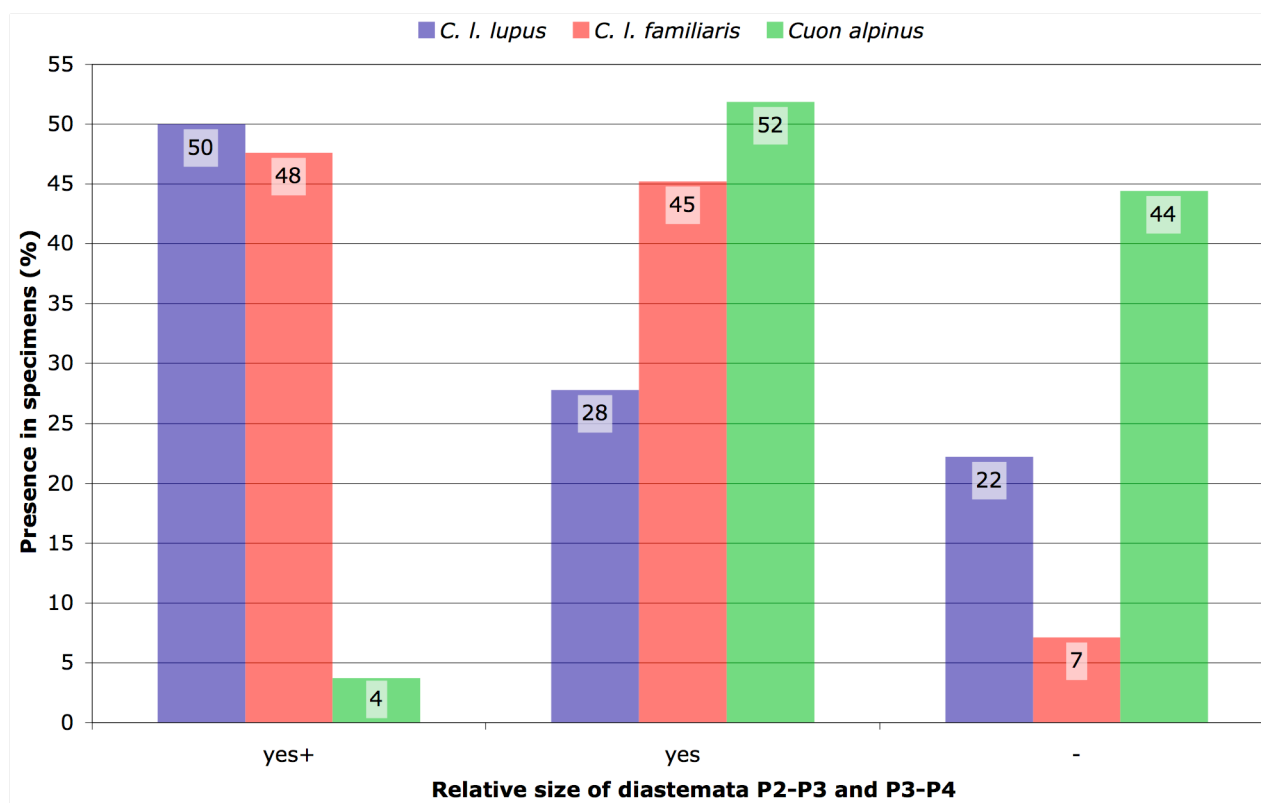
In the comparative dataset used in this study most and largest diastemata occur between the canine and the premolars. A diastema is almost always present between the canine and first premolar and often also between P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub>, although these diastemata are often smaller (fig. III.2 and appendix XIII). Between molars hardly any diastemata are observed. Additionally to the quantitative parameter of C-P<sub>1</sub>, the presence, absence and relative size of diastemata between premolars (P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub>) was recorded. It was not recorded per specimen between which premolars the diastema was positioned exactly, because this is no indication of mandible length. The main point here is to observe whether diastemata are present and if they are small or large.

##### 4.1.4.2a Results comparative material

Large diastemata are present between P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub> in about 50% of all *Canis* specimens, compared to only 4% of the *Cuon alpinus* specimens (table 4.8 and fig. 4.7). In *Cuon alpinus* absence of diastemata between premolars is much more common (44%) than in both *Canis* specimens (22% for *C. l. lupus* and only 7% for *C. l. familiaris*). Small diastemata occur in many specimens of all comparative material, but most in *Cuon alpinus* (52%), less in *C. l. familiaris* (45%) and least in *C. l. lupus* (28%). When only looking at the presence or absence of diastemata and adding up the percentages of 'yes' and 'yes+', we see that in 78% of the *C. l. lupus* specimens, 93% of the *C. l. familiaris* specimens and 56% of the *Cuon alpinus* specimens diastemata are present between the premolars. The presence of diastemata between premolars occurs thus more often in *Canis*, but also in a significant amount of the *Cuon alpinus* specimens.

**Table 4.8: Statistics of the parameter 'Diastemata' P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub> of the comparative material (absolute counted specimens (#) and %).** Diastemata were recorded as present (yes and yes+) or not present (-). 'Yes' means that the diastema was approximately equal or smaller than 2 mm. 'Yes+' means that the diastema was larger than 2 mm. Sample sizes of the comparative (sub)species were: *C. l. lupus* (18), *C. l. familiaris* (42), *Cuon alpinus* (27).

Canidae material		Relative size of diastemata P <sub>2</sub> -P <sub>3</sub> and P <sub>3</sub> -P <sub>4</sub>		
		yes+	yes	-
<i>C. l. lupus</i>	#	9	5	4
	%	50	28	22
<i>C. l. familiaris</i>	#	20	19	3
	%	48	45	7
<i>Cuon alpinus</i>	#	1	14	12
	%	4	52	44



**Figure 4.7: Bar chart of the parameter 'Mandibular diastema length' P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub> for the comparative material (in %).** For each option is indicated how much percent of the specimens of the total sample sizes of the three comparative (sub)species were encountered with that option. For absolute counted specimens, sample sizes and the legend, see table 4.8.

#### 4.1.4.2b Results fossil North Sea material

Results in the table below speak for themselves.

**Table 4.9: Presence, absence and relative size of the diastemata P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub> for the 13 fossil North Sea specimens.** ? Indicates that the presence or absence of diastemata could not be established due to a missing part of the hemimandible. 'Yes' indicates that a diastema was present and approximately equal or smaller than 2 mm. 'Yes+' means that a diastema was present and approximately larger than 2 mm.

Fossils	Relative size of diastemata P <sub>2</sub> -P <sub>3</sub> and P <sub>3</sub> -P <sub>4</sub>
534	?
535	?
667	yes
1683	yes +
2103	yes +
2104	yes +
2196	yes +
2329	yes +
2620	yes +
3219	yes +
3293	yes +
NMR89	yes
NMR90	?

## 4.1.5 Mental Foramina

Relative shortness of the mandibles of *Cuon alpinus* can be observed among other things by the middle and posterior mental foramina that are displaced one position towards distal (García and Arsuaga, 1998) (fig. III.2). According to Pérez Ripoll et al. (2010) the normal place for the middle mental foramen in *Cuon alpinus* is under P<sub>2</sub> or P<sub>2</sub> anterior and for the posterior foramen under P<sub>3</sub> or P<sub>3</sub> posterior. In *C. l. lupus* the middle mental foramen would normally be placed under the P<sub>1</sub>-P<sub>2</sub> diastema and the posterior foramen under P<sub>3</sub> anterior. These positions of the mental foramina indeed coincide with a displacement of the foramina towards distal in *Cuon alpinus* compared to *C. l. lupus* and, if results of this particular comparative dataset show a similar trend, this parameter can be used as indicator of mandible length.

### 4.1.5.1 Results comparative material

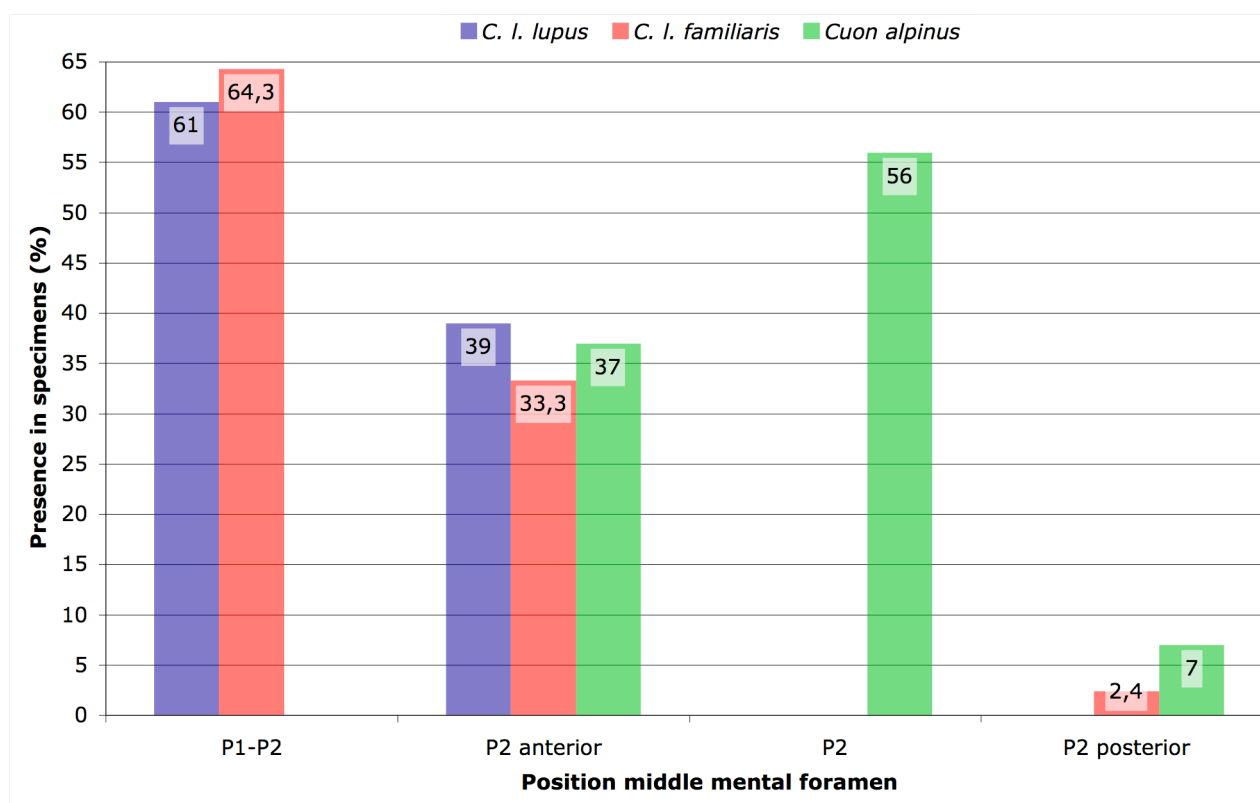
#### Middle mental foramen

In *Cuon alpinus* the middle mental foramen never occurs on a position in de mandible anterior of tooth P<sub>2</sub>, whereas for the genus *Canis* 61-64% of the middle foramina occur below teeth P<sub>1</sub>-P<sub>2</sub> (table 4.10 and fig. 4.8). The middle foramen occurs below P<sub>2</sub> anterior in similar percentages for all three comparative species: *C. l. lupus* 39%, *C. l. familiaris* 33% and *Cuon alpinus* 37%. In *C. l. lupus* and *C. l. familiaris* the middle mental foramen is never positioned below P<sub>2</sub>, but in *Cuon alpinus* quite often (56%). The position of the middle foramen under P<sub>2</sub> posterior is quite rare for all species: in *C. l. lupus* the foramen is never positioned below P<sub>2</sub> posterior, in *C. l. familiaris* rarely (2.4%) and in *Cuon alpinus* also not very often (7%). These observations compare well to the results of Pérez Ripoll et al. (2010): in almost all *Cuon alpinus* specimens the middle mental foramen is indeed positioned under P<sub>2</sub> or P<sub>2</sub> anterior (93%). Also two *Cuon alpinus* specimens were observed, in which the middle foramen was even further displaced towards distal, but the middle foramen is never positioned below P<sub>1</sub>-P<sub>2</sub>, in accordance with Pérez Ripoll et al. (2010). In *C. l. lupus* the middle mental foramen is indeed positioned below P<sub>1</sub>-P<sub>2</sub> in most cases (61%), but it was also observed that the foramen was positioned below P<sub>2</sub> anterior in a significant amount of specimens (39%). The distal displacement of the foramen in *Cuon alpinus* can also clearly be seen in fig. 4.8, where the 'peak occurrence' of *Cuon alpinus* is positioned more posterior (towards the right in the figure) than for *Canis*. There is no big difference between the fossil *C. l. familiaris* specimens from the Netherlands and the recent specimens from Suriname for this parameter. In both groups the P<sub>1</sub>-P<sub>2</sub> and P<sub>2</sub> anterior positions of the middle mental foramen are equally represented. The only difference between the two groups is, that the specimen, in which the exceptional position P<sub>2</sub> posterior is present, belongs to the recent group from the Netherlands (appendix XIII).

**Table 4.10: Statistics of the parameter 'Middle mental foramen' of the comparative material (absolute counted specimens (#) and %).** P<sub>x</sub>: foramen is positioned under the middle part of the tooth, P<sub>x</sub> anterior: foramen is positioned under the mesial part/root of the tooth, P<sub>x</sub> posterior: foramen is positioned under the distal part/root of the tooth, P<sub>x</sub>-P<sub>x</sub>: foramen is positioned in the mandible between the two specified teeth or below the diastema between these two teeth. Sample sizes of the comparative (sub)species were: *C. l. lupus* (18), *C. l. familiaris* (41), *Cuon alpinus* (27).

Canidae material		Position middle mental foramen			
		P <sub>1</sub> -P <sub>2</sub>	P <sub>2</sub> anterior	P <sub>2</sub>	P <sub>2</sub> posterior
<i>C. l. lupus</i>	#	11	7	-	-
	%	61	39	-	-
<i>C. l. familiaris</i>	#	27	13	-	1
	%	64,3	33,3	-	2,4
<i>Cuon alpinus</i>	#	-	10	15	2
	%	-	37	56	7





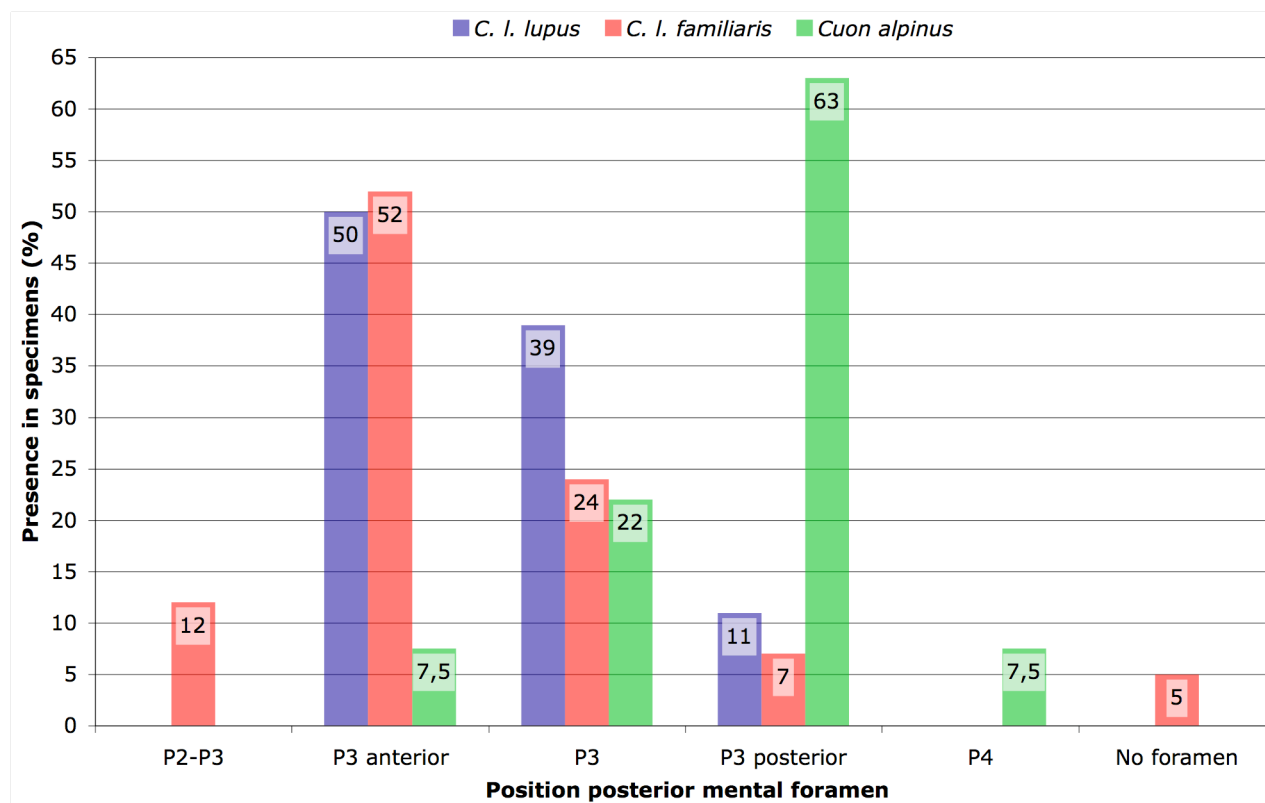
**Figure 4.8: Bar chart of the parameter ‘Middle mental foramen’ for the comparative material (in %).** For each option is indicated how much percent of the specimens of the total sample sizes of the three comparative (sub)species were encountered with that option. For absolute counted specimens, sample sizes and the legend, see table 4.10.

### Posterior mental foramen

A posterior mental foramen that is positioned below  $P_2$ - $P_3$  is only observed in *C. l. familiaris* specimens and does not occur very frequently in this species (table 4.11 and fig. 4.9). Results coincide with those of Pérez Ripoll et al. (2010) in that this position of the posterior mental foramen is not observed in *Cuon alpinus* and *C. l. lupus*. Also in coincidence with Pérez Ripoll et al. (2010) is that in both *Canis* species the posterior foramen is mostly positioned below  $P_3$  anterior (about 50% of the specimens), while in *Cuon alpinus* this does not occur often (this position is only observed in 2 specimens, table 4.11). For both *Canis* subspecies the occurrence of the posterior foramen below  $P_3$  is less frequent than for  $P_3$  anterior, but still significant (with 39% for *C. l. lupus* and 24% for *C. l. familiaris*), something Pérez Ripoll et al. (2010) did not observe. Also for *Cuon alpinus* the foramen is positioned below  $P_3$  in a significant amount of specimens (22%), which is in accordance with Pérez Ripoll et al. (2010). The  $P_3$  posterior position is typical for *Cuon alpinus*, which has its posterior foramen positioned in this place quite frequently (63%). In *Canis* the foramen is positioned below  $P_3$  posterior less frequently (with only 11% for *C. l. lupus* and 7% for *C. l. familiaris*). Compared to Pérez Ripoll et al. (2010) results coincide well for *Cuon alpinus*: the posterior mental foramen occurs mostly under  $P_3$  or  $P_3$  posterior (85%). But this foramen is not displaced towards distal in all cases ( $P_3$  anterior also occurred), although extreme distal displacement (foramen under  $P_4$ ) is also possible in *Cuon alpinus*. The displacement of the posterior mental foramen in *Cuon alpinus* is also clear from fig. 4.9: from  $P_3$  anterior to  $P_4$  the frequency of occurrence only decreases for *Canis*, while the ‘peak occurrence’ of *Cuon alpinus* is more posterior. Results of *C. l. lupus* coincide less with those of Pérez Ripoll et al. (2010):  $P_3$  anterior is indeed the position of the posterior foramen that occurs most frequently in *C. l. lupus*, but  $P_3$  and  $P_3$  posterior are also possible.  $P_3$  is thus not a typical *Cuon alpinus* position. The number of mental foramina in a mandible is highly variable and can differ per species and specimens (John de Vos, pers. comm.). It is thus also possible that the posterior foramen is absent (as in two *C. l. familiaris* specimens was the case, table 4.11). Note that, although the *number* of foramina that are present can be variable, the *position* of the foramina, if present, does show a clear trend between species, as presented above (fig. 4.9). There are no major differences between the fossil *C. l. familiaris* specimens from the Netherlands and the recent specimens from Suriname for this parameter.

**Table 4.11: Statistics of the parameter 'Posterior mental foramen' of the comparative material (absolute counted specimens (#) and %).** Legend: see table 4.10. Sample sizes of the comparative (sub)species were: *C. l. lupus* (18), *C. l. familiaris* (42), *Cuon alpinus* (27).

Canidae material		Position posterior mental foramen					
		P <sub>2</sub> -P <sub>3</sub>	P <sub>3</sub> anterior	P <sub>3</sub>	P <sub>3</sub> posterior	P <sub>4</sub>	No foramen
<i>C. l. lupus</i>	#	-	9	7	2	-	-
	%	-	50	39	11	-	-
<i>C. l. familiaris</i>	#	5	22	10	3	-	2
	%	12	52	24	7	-	5
<i>Cuon alpinus</i>	#	-	2	6	17	2	-
	%	-	7,5	22	63	7,5	-



**Figure 4.9: Bar chart of the parameter 'Posterior mental foramen' for the comparative material (in %).** For each option is indicated how much percent of the specimens of the total sample sizes of the three comparative (sub)species were encountered with that option. For absolute counted specimens, sample sizes and the legend, see table 4.11.

#### 4.1.5.2 Results fossil North Sea material

Results in table 4.12 speak for themselves. All ten fossil North Sea specimens (and also most of the comparative specimens) possess a clear and large middle mental foramen, while the posterior foramen does not stand out so clearly (appendix I). In all fossil hemimandibles the posterior foramen is just a tiny hole compared to the middle mental foramen. This was also observed in the comparative dataset: in many specimens one hemimandible would have a more clear posterior foramen, while in the other hemimandible the posterior foramen would be smaller and less pronounced. Presence and appearance (but not the positions) of mental foramina are thus indeed highly variable, also within specimens.

**Table 4.12: Position of the middle and posterior mental foramina in the fossil North Sea specimens.** Legend: see table 4.10. ? indicates that the position of the foramen could not be established due to a missing part of the hemimandible.

Fossils	Position middle mental foramen	Position posterior mental foramen
534	?	?
535	?	?
667	P1-P2	P2-P3
1683	P1-P2	P3 posterior
2103	P2 anterior	-
2104	P1-P2	P3 anterior
2196	P2 anterior	P3
2329	P1-P2	P2-P3
2620	P2 anterior	P3 posterior
3219	P2 anterior	P3
3293	P1-P2	P3 anterior
NMR89	P2 anterior	P3
NMR90	?	?

## 4.1.6 Incisors

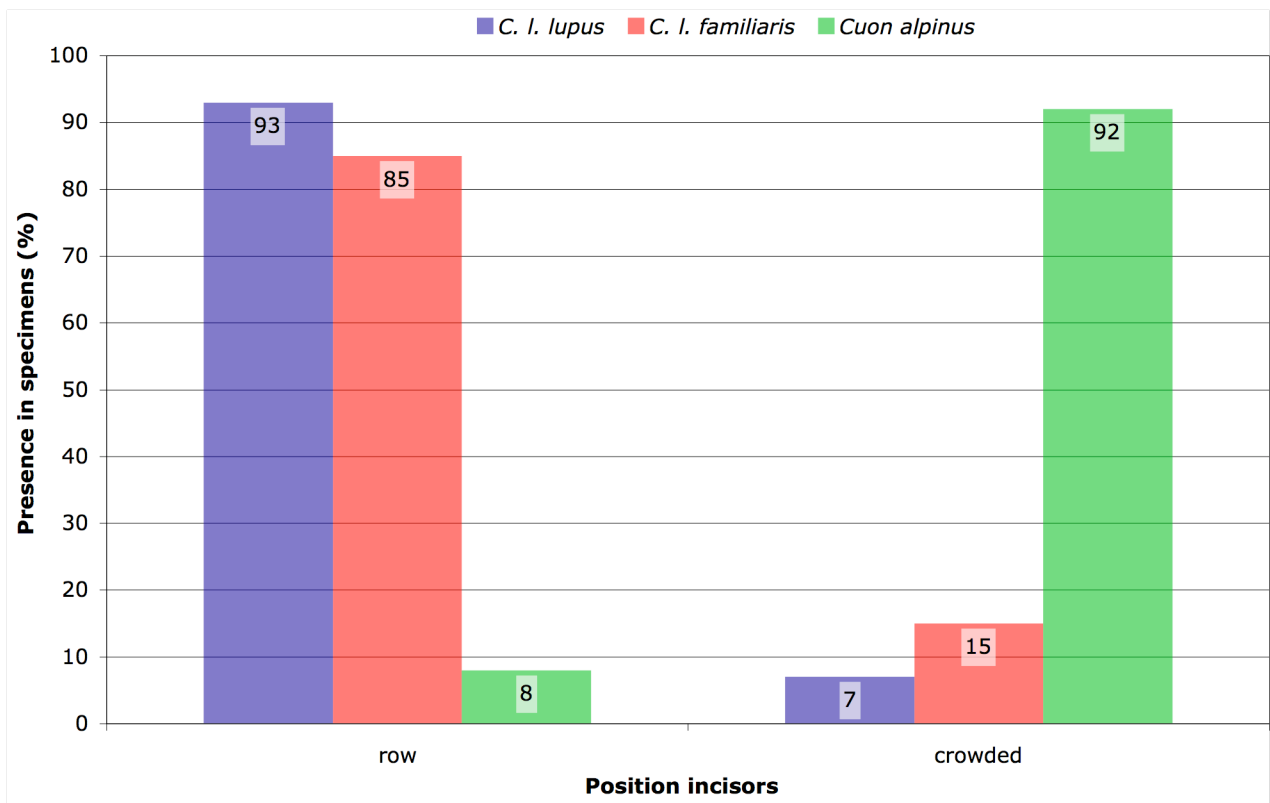
Relative shortness of the mandibles of *Cuon alpinus* can be observed among other things by the lower incisor alveoli that form an almost equilateral triangle due to crowding of the incisors (García and Arsuaga, 1998). The hypothesis is that *C. l. lupus*, which in general has a larger mandible, does not show this crowding of incisors, because there is enough space in the mandible for the incisors to be positioned in a row. *C. l. familiaris*, which has mandible lengths that coincide with both *C. l. lupus* and *Cuon alpinus* lengths will probably show more crowding than *C. l. lupus*. To test this hypothesis crowdedness of incisors was recorded for all comparative material.

### 4.1.6.1 Results comparative material

Results confirm the statement of García and Arsuaga (1998) and the hypothesis (table 4.13 and fig. 4.10). *C. l. lupus* and *Cuon alpinus* have very similar, but opposing, results: 93% of the *C. l. lupus* specimens has its incisors positioned in a row and the incisors or alveoli are often widely spaced, while in 92% of the *Cuon alpinus* specimens the incisors are crowded. The positioning of incisors in *C. l. familiaris* is very similar to that of *C. l. lupus*, with the incisors placed in a row in 85% of the specimens, although crowdedness of incisors occurs more often (and is only observed in the fossil specimens from Suriname).

**Table 4.13: Statistics of the parameter 'Incisors' of the comparative material (absolute counted specimens (#) and %).** Lower incisor alveoli can be positioned nicely in a row (row) or form an almost equilateral triangle due to crowding of the incisors (crowded). Sample sizes of the comparative (sub)species were: *C. l. lupus* (14), *C. l. familiaris* (39), *Cuon alpinus* (26).

Canidae material		Position incisors	
		row	crowded
<i>C. l. lupus</i>	#	13	1
	%	93	7
<i>C. l. familiaris</i>	#	33	6
	%	85	15
<i>Cuon alpinus</i>	#	2	24
	%	8	92



**Figure 4.10: Bar chart of the parameter 'Incisors' for the comparative material (in %).** For each option is indicated how much percent of the specimens of the total sample sizes of the three comparative (sub)species were encountered with that option. For absolute counted specimens, sample sizes and the legend, see table 4.13

#### **4.1.6.2 Results fossil North Sea material**

Almost all fossil North Sea specimens miss the most anterior part of the hemimandible, in which the incisors are placed (appendix I). Only for specimens 2104, 2620 and 3219 could be determined how incisors were positioned. Specimen 2104 and 3219 both show 2-3 incisor alveoli that are positioned nicely in a row (plate 4.1 and appendix XIII). Specimen 2620 still possesses two incisors and these are also positioned in a row (appendix XIII).

## 4.2 Mandible (width, height and ratios)

### 4.2.1 Mandible width *i-i'* and *k-k'*

#### 4.2.1.1 Results comparative material

For all values see table 4.14 and fig. 4.11 unless stated otherwise.

**x** With 14.57 mm *C. l. lupus* has on average the largest mandible width (*i-i'*, fig. IV.2), followed by *C. l. familiaris* (11.4 mm) and *Cuon alpinus* (11.2 mm). The *Cuon alpinus* and *C. l. familiaris* means lie closer together than the means of both *Canis* species. Values are similar for *k-k'* (table 4.14 and fig. 4.11). These observations are in accordance with the statement of Pérez Ripoll et al. (2010) that mandibles of *C. l. lupus* are mostly wider than those of *Cuon alpinus*.

**SD vs. n** For both parameters the trend of the standard deviation is the same as for parameters *a-b* and *c-b*: *C. l. familiaris* shows the greatest variation in mandible width (SD of 2.06 mm and largest range in fig. 3.16), while this species also has the greatest sample size (n 42). *C. l. lupus*, the species with the lowest sample size (n 18), shows more variation (SD of 1.69 mm) than *Cuon alpinus* (SD 0.86 mm), which has a much greater sample size (n 27) than *C. l. lupus* (table 4.14).

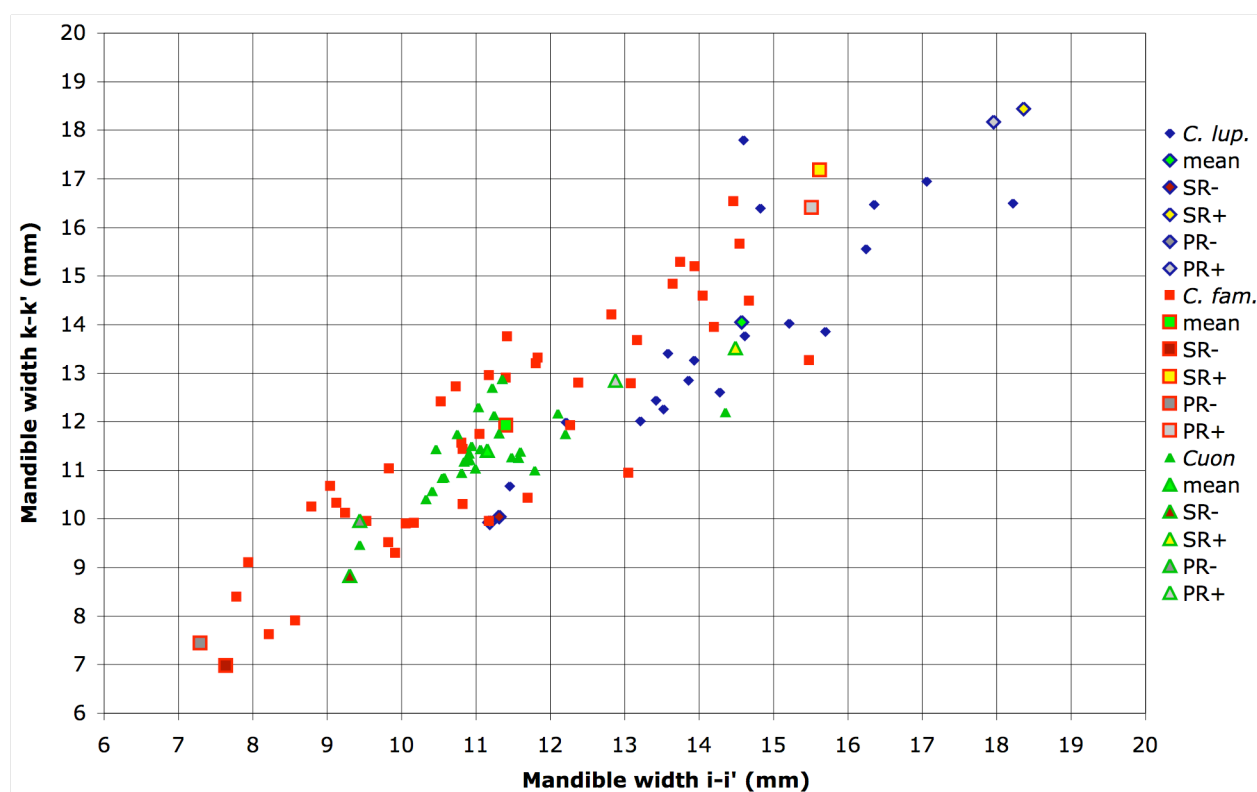
**Sample range** For all values of the sample ranges see table 4.14. All sample ranges overlap significantly (a few mm) for these two parameters. The *Cuon alpinus* sample range falls entirely within the *C. l. familiaris* sample range and overlaps with *C. l. lupus* in the upper part of its range. The *Cuon alpinus* maximum even plots very close to the *C. l. lupus* mean and the *C. l. lupus* minimum plots below the *Cuon alpinus* mean (fig. 4.11). Only the smallest *Cuon alpinus* mandibles fall outside the *C. l. lupus* sample range. Although there is much overlap between the *Cuon alpinus* and *C. l. lupus* ranges, an apparent separation of the *Cuon alpinus* and *C. l. lupus* data clouds can be seen in fig. 4.11, whereby most *C. l. lupus* specimens plot in the upper right quadrant and most *Cuon alpinus* specimens in the lower left quadrant of the figure. The data cloud of *C. l. familiaris* is very large and plots over almost the entire range of the graph: specimens plot from lower than the *Cuon alpinus* minimum to larger than the *C. l. lupus* mean. For these two parameters there is a quite clear separation within the *C. l. familiaris* group between the fossil specimens from the Netherlands and the recent specimens from Suriname, when looking at the combination of the two parameters in fig. VII.4. The smallest *C. l. familiaris* mandibles are recent specimens from Suriname and the widest mandibles are fossil specimens from the Netherlands. There is a lot of spread in specimens for parameters *i-i'* and *k-k'* (fig. 4.11). The *C. l. familiaris* data cloud is large and broad, but the specimens plot quite evenly over its range (there is a similar density of specimens over the entire range) and there are no extremely deviating specimens. *Cuon alpinus* specimens are more centered in a data cloud, from which two *Cuon alpinus* specimens deviate a little: specimen 945 (approximate coordinates 14, 12 mm) has a relative high value for *i-i'* compared to its value for *k-k'* and *cuon-h* (9, 9 mm) has relative small mandibles with respect to both parameters and plots below the average *Cuon alpinus* cloud. The *C. l. lupus* data cloud becomes more and more spread in the upper part of its range and there is not a specific specimen that deviates much from an imaginary linear trend line, since all specimens in the upper part of the range are widely spread.

**Population ranges** for the two parameters can also be found in table 4.14. Even for the population ranges all three comparative species still overlap significantly with each other. *Cuon alpinus* still plots entirely within the *C. l. familiaris* range and well within the *C. l. lupus* population range; the *Cuon alpinus* minimum value is only slightly smaller than the *C. l. lupus* minimum for *i-i'* and even larger than the *C. l. lupus* minimum for *k-k'*. *C. l. familiaris* still plots over a large range, from much lower than the *Cuon alpinus* minimum to much larger than the *C. l. lupus* mean.

**Trend lines** Both *Canis* specimens have slightly less variation (lower standard deviations) in *i-i'* than in *k-k'*, while for *Cuon alpinus* this results is reversed (table 4.14 and fig. 4.11). In general both parameters are quite similar and are well comparable, although spread of data points is high for these parameters. For this reason, trend lines are not plotted; they are not helpful in the determination of the identity of the fossil North Sea specimens.

**Table 4.14: Statistics of the parameters 'Mandible width' *i-i'* (left) and *k-k'* (right) of the comparative material (in mm).** Legend: see table 4.1.

Statistics	Mandible with <i>i-i'</i>			Mandible with <i>k-k'</i>		
	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>
Sample size (n)	18	42	27	18	42	27
Sample mean (x)	14,57	11,4	11,2	14,05	11,9	11,4
Standard deviation (SD)	1,69	2,06	0,86	2,06	2,24	0,72
Minimum (MIN)	11,45	7,78	9,44	10,68	7,62	9,47
Maximum (MAX)	18,22	15,5	14,4	17,80	16,5	12,9
Sample range MIN	11,31	7,64	9,30	10,04	6,98	8,83
Sample range MAX	18,36	15,6	14,5	18,44	17,2	13,5
Population range MIN	11,18	7,29	9,43	9,92	7,44	9,96
Population range MAX	17,96	15,5	12,9	18,17	16,4	12,8



**Figure 4.11: Scatter plot of parameters 'Mandible width' *i-i'* vs. *k-k'* for the comparative material (in mm).** Legend, see table 4.1.

#### 4.2.1.2 Results fossil North Sea material

Not all 13 fossil North Sea specimens had values for both parameters, thus only 8 specimens could be plotted in the fig. 4.12 below.

##### Specimen 534

Specimen 534 misses the mandibular body anterior of  $M_2$ , thus parameters 'Mandible width' *i-i'* and *k-k'* could not be taken on this specimen (appendix I).

##### Specimen 535

Specimen 535 misses a large anterior part of its hemimandible as a result of which parameter *k-k'* could not be taken (appendix I). Specimen 535 is not plotted in fig. 4.12, because it only has a value for *i-i'*. The specimen range of 535 falls entirely within the sample and population ranges of all comparative material for this parameter (table 4.15 and fig. 4.12). The mean value of specimen 535 (12.32 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.92 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 1.17 mm) and most dissimilar to the average *C. l. lupus* (2.25 mm) (appendix XIII).

**Specimen 667**

The specimen range of 667 falls entirely within all sample and population ranges of all comparative species (fossil part of the *C. l. familiaris* sample range), except the population range of *Cuon alpinus* for parameter  $k-k'$  (table 4.15 and fig. 4.12). Specimen 667 overlaps for most part of its range (0.91 mm) with this population range, but also partly not (0.37 mm above the *Cuon alpinus* maximum). This overlap with all three comparative species is very obvious in fig. 4.12, where specimen 667 plots in the middle of the graph. The mean value of specimen 667 for  $i-i'$  (12.34 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.94 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 1.19 mm) and most dissimilar to the average *C. l. lupus* (2.23 mm) (appendix XIII). Values are similar for parameter  $k-k'$ .

**Specimen 1683**

Specimen 1683 falls within the sample and population ranges of *C. l. lupus* and outside (above) the sample and population range of *Cuon alpinus* for both parameters (table 4.15 and fig. 4.12). For parameter  $i-i'$  1683 falls entirely outside (above) the sample and population range of *C. l. familiaris*, but for parameter  $k-k'$  1683 falls entirely within the *C. l. familiaris* sample range and for most part within the population range. The mean value of specimen 1683 for  $i-i'$  (16.91 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 2.34 mm between the two mean values) and more dissimilar to *C. l. familiaris* (5.51 mm) and *Cuon alpinus* (5.76 mm) (see fig. 4.12). Values are similar for parameter  $k-k'$ .

**Specimen 2103**

Specimen 2103 falls within the sample and population ranges of *C. l. familiaris* for both parameters (fossil part), within the sample and population ranges of *C. l. lupus* for  $k-k'$  and within the sample and population ranges of *Cuon alpinus* for  $i-i'$  (table 4.15 and fig. 4.12). The specimen range of 2103 falls entirely outside (below) the *C. l. lupus* sample range and for most part outside (below) the *C. l. lupus* population range for parameter  $i-i'$  and entirely inside the sample range of *Cuon alpinus* and for most part inside the *Cuon alpinus* population range for parameter  $k-k'$ . The mean value of specimen 2103 for  $i-i'$  (11.06 mm) is very similar to the average *Cuon alpinus* specimen (with a distance of 0.09 mm between the two mean values), less similar to the average *C. l. familiaris* specimen (with 0.34 mm) and most dissimilar to the average *C. l. lupus* specimen (appendix XIII). This trend is different for parameter  $k-k'$ : in this parameter the mean value of specimen 2103 (12.46 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.54 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (0.54 mm) and least similar to *C. l. lupus* (1.59 mm) (fig. 4.12).

**Specimen 2104**

The specimen range of 2104 falls within the sample and population ranges of all comparative species for both parameters as is also obvious from its position in fig. 4.12 (fossil part of the *C. l. familiaris* sample range, fig. VII.4). The mean value of specimen 2104 for parameter  $i-i'$  (11.70 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.30 mm between the two mean values), less similar to the average *Cuon alpinus* (0.55 mm) and least similar to the average *C. l. lupus* specimen (2.87 mm) (appendix XIII).

**Specimen 2196**

Specimen 2196 falls entirely within the sample and population ranges of *C. l. lupus* for parameter  $i-i'$  and entirely outside (above) the sample and population ranges of *C. l. familiaris* (for parameter  $i-i'$ ) and *Cuon alpinus* (both parameters) (table 4.15 and fig. 4.12). Specimen 2196 falls also within the *C. l. lupus* sample range for parameter  $k-k'$  and even slightly above the population range. Specimen 2196 falls for most part of its range outside (above) the *C. l. familiaris* sample range for  $k-k'$  and entirely outside (above) the population range. The mean value of specimen 2196 for parameter  $i-i'$  (15.85 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 1.28 mm between the two mean values) and much less similar to the average *C. l. familiaris* (4.45 mm) and *Cuon alpinus* (4.70 mm) specimens (fig. 4.12). Mean values are similar for  $k-k'$ .

**Specimen 2329**

The specimen range of 2329 falls entirely within the sample and population ranges of both *Canis* species for both parameters (table 4.15 and fig. 4.12). Specimen 2329 also falls within the sample range of *Cuon alpinus* for parameter  $i-i'$ , but outside (above) the *Cuon alpinus* population range for this parameter. Specimen 2329 also falls outside (above) the sample and population range of *C. l. familiaris* for  $k-k'$ . The mean value of specimen 2329 for parameter  $i-i'$  (13.07 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 1.50 mm between the two mean values), less similar to the average *C. l. familiaris* specimen (1.67 mm) and least similar to the average *Cuon alpinus* specimen (1.92 mm) (fig. 4.12). This trend is the same for parameter  $k-k'$ , but the differences between the distances between the two mean values of the three comparative species are slightly larger.

### **Specimen 2620**

The specimen range of 2620 falls entirely within the sample and population ranges of both *Canis* species for parameter  $i-i'$  and of *C. l. lupus* for parameter  $k-k'$  (table 4.15 and fig. 4.12). Specimen 2620 falls entirely outside (above) the *Cuon alpinus* sample and population ranges for both parameters and for most part inside the *C. l. familiaris* sample range and for most part outside (above) the *C. l. familiaris* population range for parameter  $k-k'$ . The mean value of specimen 2620 for parameter  $i-i'$  (14.90 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.33 mm between the two mean values) and more dissimilar to the average *C. l. familiaris* (3.50 mm) and *Cuon alpinus* (3.75 mm) specimens (appendix XIII). This trend is the same for parameter  $k-k'$ .

### **Specimen 3219**

The specimen range of 3219 falls entirely within the sample and population ranges of all comparative material for both parameters (fossil part of the *C. l. familiaris* sample range), except in the *Cuon alpinus* sample and population ranges for parameter  $k-k'$  (table 4.15 and fig. 4.12). The width of the mandible of specimen 3219 is larger than the maxima of those two ranges (fig. 4.12). The mean value of specimen 3219 for parameter  $i-i'$  (12.47 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 1.07 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 1.31 mm) and most dissimilar to the average *C. l. lupus* specimen (2.10 mm) (appendix XIII). This trend is different for parameter  $k-k'$ : for this parameter specimen 3219 is most similar to the average *C. l. lupus* specimen (with a distance of 0.87 mm between the two mean values), less similar to the average *C. l. familiaris* specimen (2.97 mm) and most dissimilar to the average *Cuon alpinus* (3.48 mm).

### **Specimen 3293**

Specimen 3293 misses its most anterior part of the mandible, where the symphyse is located as a result of which parameter  $k-k'$  could not be taken (appendix I). Specimen 3293 is not plotted in fig. 4.12, because it only has a value for  $i-i'$ . The specimen range of 3293 falls entirely within the sample and population ranges of *C. l. lupus* and also (for most part) within the *C. l. familiaris* sample and population ranges (table 4.15 and fig. 4.12). Specimen 3293 falls entirely outside (above) the sample and population ranges of *Cuon alpinus*. The mean value of specimen 3293 for  $i-i'$  (15.40 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.83 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* (4.00 mm) and *Cuon alpinus* (4.25 mm) specimens (fig. 4.12 and appendix XIII).

### **Specimen NMR89**

NMR89 misses its most anterior part of the mandible, where the  $P_1$  and symphyse are located, thus parameter  $k-k'$  could not be taken (appendix I). Specimen NMR89 is not plotted in fig. 4.12, because it only has a value for  $i-i'$ . Specimen NMR89 falls entirely within the sample and population ranges of all comparative material, except within the *Cuon alpinus* population range: NMR89 falls slightly outside (above) this range. The mean value of NMR89 for  $i-i'$  (12.80 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 1.40 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (1.65 mm) and least similar to the average *C. l. lupus* specimen (1.77 mm) (appendix XIII).

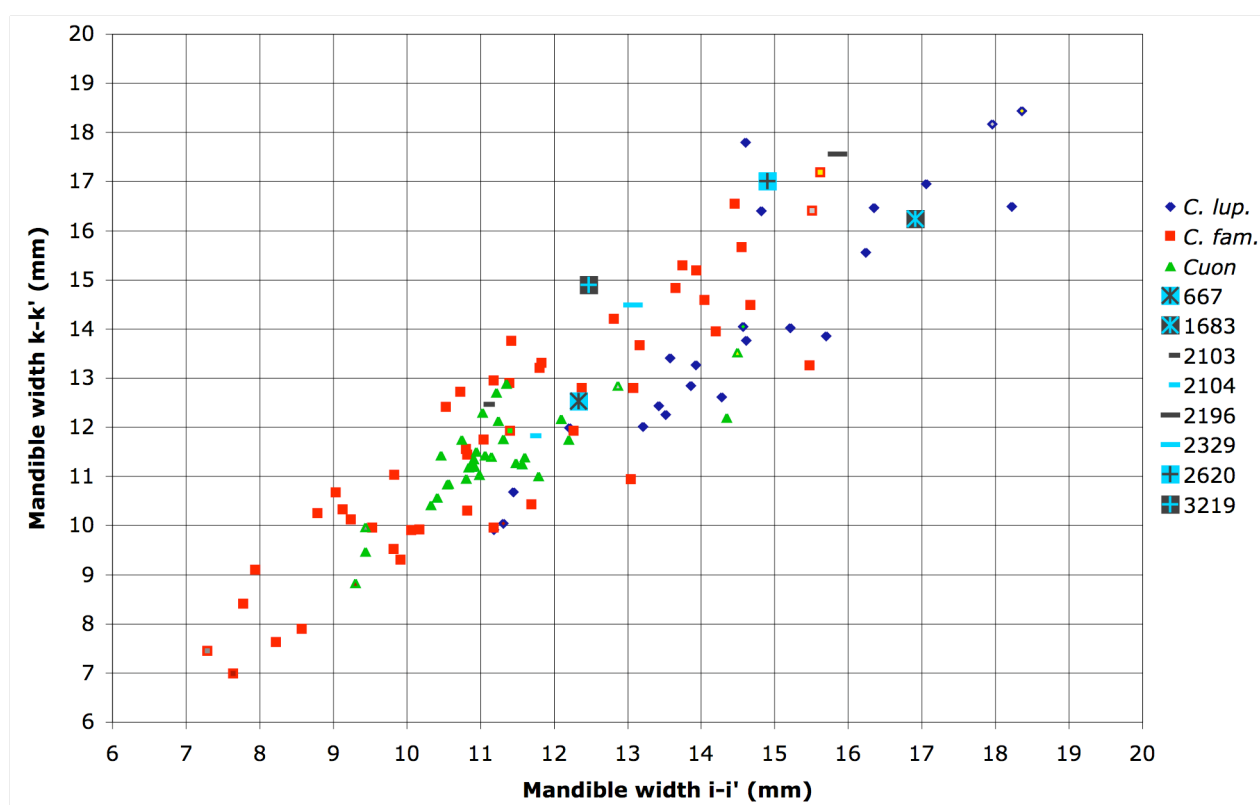
### **Specimen NMR90**

Specimen NMR90 misses a large anterior part of its hemimandible as a result of which parameter  $k-k'$  could not be taken (appendix I). NMR90 is also not plotted in fig. 4.12, because it only has a value for  $i-i'$ . The specimen range of NMR90 falls entirely in all sample and population ranges of all three comparative species (table 4.15 and fig. 4.12). The mean value of NMR90 for  $i-i'$  (12.37 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.97 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (1.22 mm) and least similar to the average *C. l. lupus* specimen (2.20 mm) (appendix XIII).



**Table 4.15: Comparison of the specimen ranges of the fossil North Sea specimens with the sample and population ranges of the comparative material for parameters 'Mandible width'  $i-i'$  (left) and  $k-k'$  (right) (in mm).** Sample and population ranges of the comparative material are as given in table 4.14. Specimen ranges were calculated as explained in table 4.2.

Canidae material		Mandible with $i-i'$				Mandible with $k-k'$			
		- Sample range +		- Population range +		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	11,31	18,36	11,18	17,96	11,31	18,36	11,18	17,96
	<i>C. l. familiaris</i>	7,64	15,6	7,29	15,5	7,64	15,6	7,29	15,5
	<i>Cuon alpinus</i>	9,30	14,5	9,43	12,9	9,30	14,5	9,43	12,9
Fossil North Sea	535	12,18	12,46	-	-	-	-	-	-
	667	12,20	12,48	-	-	11,89	13,17	-	-
	1683	16,77	17,05	-	-	15,60	16,88	-	-
	2103	10,92	11,20	-	-	11,82	13,10	-	-
	2104	11,56	11,84	-	-	11,18	12,46	-	-
	2196	15,71	15,99	-	-	16,92	18,20	-	-
	2329	12,93	13,21	-	-	13,85	15,13	-	-
	2620	14,76	15,04	-	-	16,37	17,65	-	-
	3219	12,33	12,61	-	-	14,25	15,53	-	-
	3293	15,26	15,54	-	-	-	-	-	-
	NMR89	12,66	12,94	-	-	-	-	-	-
	NMR90	12,23	12,51	-	-	-	-	-	-



**Figure 4.12: Scatter plot of parameters 'Mandible width'  $i-i'$  vs.  $k-k'$  for the fossil North Sea specimens and the comparative material (in mm).** Legend, see tables 4.1 and 4.2.

## 4.2.2 Mandible height $h-h'$ under $P_1$ and $P_2$

### 4.2.2.1 Results comparative material

For all values see both table 4.16 and fig. 4.13 unless stated otherwise.

**x** For both parameters *C. l. lupus* has on average the largest mandible height under  $P_1$  and  $P_2$  (fig. IV.1) (with 25.59 mm for  $h-h'$   $P_1$ ), while both *C. l. familiaris* and *Cuon alpinus* have significantly smaller heights and lie closer together (with 19.89 mm and 18.98 mm respectively, table 4.16).

**SD vs. n** *C. l. familiaris* shows the greatest variation in mandible height (SD of 3.24 mm and largest range in fig. 3.18), while this species also has the greatest sample size (n 42). *C. l. lupus*, the species with the lowest sample size (n 18), shows more variation (SD 2.82 mm) than *Cuon alpinus* (SD 1.42 mm), which has a much greater sample size (n 26) than *C. l. lupus* and the lowest amount of variation of all three comparative species (table 4.16). Values are very similar for parameter  $h-h'$   $P_2$ .

**Sample ranges** of *Cuon alpinus* and *C. l. lupus* slightly overlap in the upper part of the *Cuon alpinus* range (a little less for  $h-h'$   $P_1$  than for  $P_2$ ) (table 4.16). *Cuon alpinus* plots in general in the lower parts of fig. 4.13, while *C. l. lupus* occupies the upper regions. *C. l. familiaris* shows the largest range of heights and plots from (slightly) lower than the *Cuon alpinus* minimum to close to the *C. l. lupus* mean, overlapping significantly with both species. Also for these parameters a distinction can be made within the *C. l. familiaris* group, separating the fossil specimens from the Netherlands from the recent specimens from Suriname. As was the trend for previous parameters the *C. l. familiaris* specimens with the smallest heights are all recent specimens from Suriname and the upper *C. l. familiaris* range consist mostly of fossil specimens from the Netherlands (fig. VII.5). Data points of all comparative species plot evenly over their ranges in a quite linear way, although one *Cuon alpinus* specimen (945 with approximate coordinates 20, 24) is slightly isolated from the broad linear band of specimens, because it has a relative high height below  $P_2$  compared to its height below  $P_1$  (fig. 4.13).

**Population ranges** see table 4.16. Also for the population ranges there is still some overlap between the *Cuon alpinus* and *C. l. lupus* ranges. *C. l. familiaris* still overlaps significantly with these both species, with its minimum plotting below the *Cuon alpinus* minimum and its maximum plotting close to the *C. l. lupus* mean in fig. 4.13.

**Trend lines** The amount of spread of data points (standard deviation) is very similar for both parameters; the standard deviation of *C. l. lupus* even is the same for  $P_1$  and  $P_2$  (table 4.16 and fig. 4.13). The two parameters are thus very well comparable. On first sight the specimens of all comparative species seem to plot in a broad linear band, but after closer examination *C. l. lupus* specimens on average appear to have a slightly larger height under  $P_2$  than *Cuon alpinus* and *C. l. familiaris*, of which the trend lines plot very closer together (fig. VIII.3). This slightly different position of the *C. l. lupus* versus *C. l. familiaris* and *Cuon alpinus* data clouds might be a visual aid in the determination of the fossil North Sea specimens. No significant distinction can be made between *C. l. familiaris* and *Cuon alpinus* based on trend lines.

**Table 4.16: Statistics of the parameters 'Mandible height  $h-h'$ '  $P_1$  (left) and  $P_2$  (right) of the comparative material (in mm).** Legend: see table 4.1.

Statistics	Mandible height $h-h'$ $P_1$			Mandible height $h-h'$ $P_2$		
	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>
Sample size (n)	18	42	26	17	42	27
Sample mean (x)	25,59	19,89	18,98	27,20	20,00	19,33
Standard deviation (SD)	2,82	3,24	1,42	2,82	3,32	1,82
Minimum (MIN)	21,28	13,50	14,58	22,66	13,72	13,77
Maximum (MAX)	29,87	25,47	21,78	32,23	26,53	24,61
Sample range MIN	21,00	13,22	14,30	22,38	13,44	13,49
Sample range MAX	30,15	25,75	22,06	32,51	26,81	24,89
Population range MIN	19,95	13,42	16,13	21,56	13,36	15,68
Population range MAX	31,22	26,36	21,82	32,84	26,65	22,98

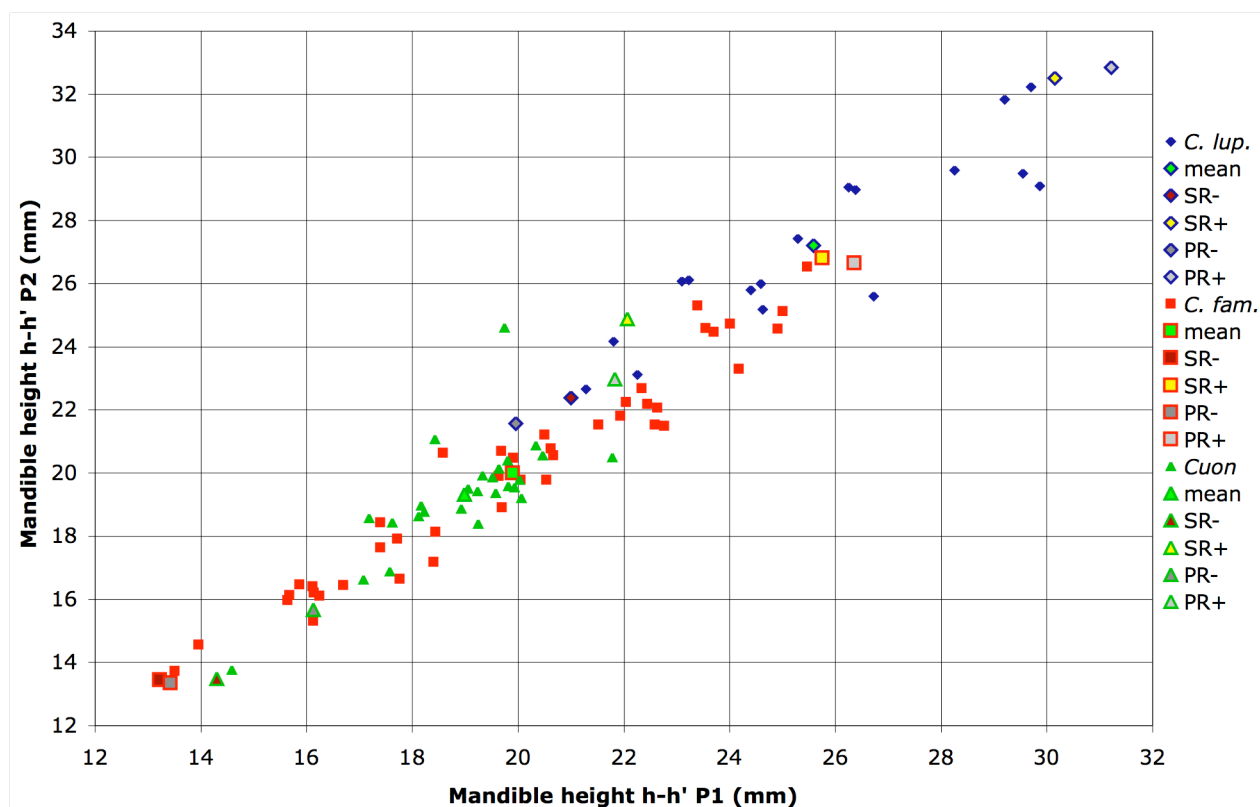


Figure 4.13: Scatter plot of parameters 'Mandible height  $h-h'$  P<sub>1</sub> vs. P<sub>2</sub> for the comparative material (in mm). Legend, see table 4.1.

#### 4.2.2.2 Results fossil North Sea material

Not all 13 fossil North Sea specimens had values for both parameters, thus only 9 specimens could be plotted in fig. 4.14.

##### Specimen 534, 535 and NMR90

These three specimens miss a large anterior part of their hemimandible, thus no data is available for parameters  $h-h'$  P<sub>1</sub> and P<sub>2</sub> for 534, 535 and NMR90 (appendix I).

##### Specimen 667

Specimen 667 falls entirely within the sample and population ranges of *C. l. familiaris* (fossil part) and *Cuon alpinus* for both parameters, while it falls entirely outside (below) the sample ranges of *C. l. lupus* (table 4.17 and fig. 4.14). It also falls entirely outside (below) the *C. l. lupus* population range for parameter  $h-h'$  P<sub>2</sub>, but slightly overlaps with the lower part of the *C. l. lupus* population range for  $h-h'$  P<sub>1</sub>. The mean value of 667 for  $h-h'$  P<sub>1</sub> and P<sub>2</sub> (20.10 respectively 19.60 mm) is most dissimilar to the average *C. l. lupus* specimen (with a distance of 5.49 mm respectively 7.60 mm between the two mean values) (appendix XIII). Results are reversed for *C. l. familiaris* and *Cuon alpinus* for both parameters: for  $h-h'$  P<sub>1</sub> 667 is most similar to the average *C. l. familiaris* specimen (0.21 mm) and less similar to the average *Cuon alpinus* specimen (1.12 mm), while for  $h-h'$  P<sub>2</sub> 667 is most similar to the average *Cuon alpinus* specimen (0.27 mm) and less similar to the average *C. l. familiaris* specimen (0.40 mm). Specimen 667 plots in the middle of the *C. l. familiaris* and *Cuon alpinus* clouds, relatively far away from the *C. l. lupus* data cloud, close to the *C. l. familiaris* and *Cuon alpinus* trend lines (fig. VIII.3).

##### Specimen 1683

Specimen 1683 falls entirely outside (above) the sample and population ranges of *Cuon alpinus* and *C. l. familiaris* and entirely within the sample and population ranges of *C. l. lupus* (table 4.17 and fig. 4.14). Specimen 1683 is thus most similar to the average *C. l. lupus* specimen (with a distance of 2.67 mm between the two mean values for  $h-h'$  P<sub>1</sub>) and much more dissimilar to *C. l. familiaris* and *Cuon alpinus* (with an average distance of 9-10 mm) (appendix XIII). Specimen 1683 is slightly more similar to *C. l. familiaris* for  $h-h'$  P<sub>1</sub> and slightly more similar to *Cuon alpinus* for  $h-h'$  P<sub>2</sub>. Specimen 1683 plots in the upper part of fig. VIII.3, close to the *C. l. lupus* trend line and far above the *C. l. familiaris* and *Cuon alpinus* data clouds.

### Specimen 2103

The specimen range of 2103 falls entirely within the sample and population ranges of *C. l. lupus* for parameter  $h-h' P_2$ , of *C. l. familiaris* for both parameters (fossil part) and of *Cuon alpinus* for parameter  $h-h' P_1$  (table 4.17, fig. 4.14 and fig. VII.5). It also falls entirely within the *C. l. lupus* population range for  $h-h' P_1$  and within the *Cuon alpinus* sample range for  $h-h' P_2$ . Specimen 2103 only slightly overlaps with the lower part of the sample range of *C. l. lupus* for  $h-h' P_1$  and overlaps for most part with the upper part of the *Cuon alpinus* population range for parameter  $h-h' P_2$ . The mean value of specimen 2103 for parameter  $h-h' P_1$  (20.91 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 1.02 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 1.93 mm) and most dissimilar to the average *C. l. lupus* specimen (4.68 mm) (appendix XIII). This trend is the same for parameter  $h-h' P_2$ . Specimen 2103 does not plot significantly closer to one of the trend lines of the comparative species in fig. VIII.3.

### Specimen 2104

Specimen 2104 falls entirely within the sample and population ranges of both *Canis* species for both parameters (fossil part of the *C. l. familiaris* sample range, fig. VII.5), entirely outside (above) the *Cuon alpinus* sample and population range for  $h-h' P_1$  and entirely within the *Cuon alpinus* sample range for  $h-h' P_2$  (table 4.17 and fig. 4.14). Specimen 2104 partly falls outside (above) the *Cuon alpinus* population range for  $h-h' P_2$ . The mean value of specimen 2104 for parameter  $h-h' P_1$  (22.64 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 2.75 mm between the two mean values), slightly less similar to the average *C. l. lupus* specimen (with 2.95 mm) and most dissimilar to the average *Cuon alpinus* specimen (3.66 mm) (appendix XIII). Values are similar for parameter  $h-h' P_2$ , with the exception that 2104 is more similar to *Cuon alpinus* than to *C. l. lupus*. 2104 Plots exactly on the *C. l. familiaris* trend line, which is in the middle of fig. VIII.3 and not significantly far away from either *Cuon alpinus* or *C. l. lupus* data clouds.

### Specimen 2196

The specimen range of 2196 falls entirely outside (above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* and entirely within all *C. l. lupus* ranges for both parameters (table 4.17 and fig. 4.14). Specimen 2196 is thus more similar to the average *C. l. lupus* specimen (with a distance of 3.31 mm between the two mean values) than to the average *C. l. familiaris* (9.01 mm) or *Cuon alpinus* (9.92 mm) specimens (appendix XIII). This trend is the same for parameter  $h-h' P_2$ . Specimen 2196 plots in the upper part of fig. VIII.3, close to the *C. l. lupus* trend line and far above the *C. l. familiaris* and *Cuon alpinus* data clouds.

### Specimen 2329

The specimen range of 2329 falls entirely within the sample and population ranges of *C. l. lupus* and entirely outside (above) the *Cuon alpinus* sample and population ranges for both parameters (table 4.17 and fig. 4.14). Specimen 2329 also falls entirely within the sample and population range of *C. l. familiaris* for parameter  $h-h' P_1$  and within the sample range for  $h-h' P_2$ . Specimen 2329 partly falls outside (above) the population range of *C. l. familiaris* for parameter  $h-h' P_2$ . The mean value of specimen 2329 for parameter  $h-h' P_1$  (24.72 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.87 mm between the two mean values), much less similar to the average *C. l. familiaris* specimen (with 4.83 mm) and most dissimilar to the average *Cuon alpinus* specimen (5.74 mm) (appendix XIII). This trend is the same for parameter  $h-h' P_2$ . Specimen 2329 plots exactly on the *C. l. lupus* trend line in fig. VIII.3.

### Specimen 2620

Specimen 2620 falls entirely outside (above) the *Cuon alpinus* and *C. l. familiaris* sample and population ranges for both parameters, but within the sample and population ranges of *C. l. lupus* (table 4.17 and fig. 4.14). Specimen 2620 even falls slightly outside (above) the *C. l. lupus* sample range for parameter  $h-h' P_2$ . The mean value of specimen 2620 for parameter  $h-h' P_1$  (29.66 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 4.07 mm between the two mean values), much less similar to the average *C. l. familiaris* specimen (with 9.77 mm) and most dissimilar to the average *Cuon alpinus* specimen (10.68 mm) (appendix XIII). Values are similar for parameter  $h-h' P_2$ . This specimen plots in the uppermost part of fig. VIII.3, closest to the *C. l. lupus* trend line and far above the *C. l. familiaris* and *Cuon alpinus* data clouds.

### Specimen 3219

Specimen 3219 falls entirely within the sample and population ranges of all comparative material for both parameters (fossil part of the *C. l. familiaris* sample range), except the *C. l. lupus* sample range of parameter  $h-h' P_2$ , for which the overlap is only partly (table 4.17, fig. 4.14 and fig. VII.5). The mean value of specimen 3219 for parameter  $h-h' P_1$  (21.39 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 1.50 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 2.41 mm) and most dissimilar to the average *C. l. lupus* specimen (4.20 mm) (appendix XIII). This trend is

the same for parameter  $h-h'$  P<sub>2</sub>. Specimen 3219 plots in the middle of fig. VIII.3, closer to *C. l. familiaris* and *Cuon alpinus* trend lines than to that of *C. l. lupus*.

### Specimen 3293

Specimen 3293 falls entirely outside (above) the *Cuon alpinus* sample and population ranges and entirely within the sample and population ranges of both *Canis* species for both parameters, although 3293 falls within the upper most part of the *C. l. familiaris* ranges (table 4.17 and fig. 4.14). The mean value of specimen 3293 for parameter  $h-h'$  P<sub>1</sub> (24.93 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.66 mm between the two mean values) and much less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with respectively 5.04 and 5.95 mm) (appendix XIII). Values are similar for parameter  $h-h'$  P<sub>2</sub>. Specimen 3293 plots very close to the *C. l. lupus* trend line, above the *Cuon alpinus* data cloud (fig. VIII.3).

### Specimen NMR89

Specimen NMR89 only has values for parameter  $h-h'$  P<sub>2</sub> and is thus not plotted in fig. 4.14. NMR89 falls entirely within the *C. l. familiaris* and *Cuon alpinus* sample and population range and entirely outside (below) the *C. l. lupus* sample and population range (table 4.17). The mean value of NMR89 for parameter  $h-h'$  P<sub>2</sub> (18.64 mm) is most similar to the average *Cuon alpinus* specimen (with a distance of 0.69 mm between the two mean values), less similar to the average *C. l. familiaris* specimen (1.36 mm) and much more dissimilar to the average *C. l. lupus* specimen (8.56 mm) (appendix XIII).

**Table 4.17: Comparison of the specimen ranges of the fossil North Sea specimens with the sample and population ranges of the comparative material for parameters 'Mandible height  $h-h'$ ' P<sub>1</sub> (left) and P<sub>2</sub> (right) (in mm). Sample and population ranges of the comparative material are as given in table 4.16. Specimen ranges were calculated as explained in table 4.2.**

Canidae material		Mandible height $h-h'$ P <sub>1</sub>				Mandible height $h-h'$ P <sub>2</sub>			
		- Sample range +		- Population range +		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	21,00	30,15	19,95	31,22	22,38	32,51	21,56	32,84
	<i>C. l. familiaris</i>	13,22	25,75	13,42	26,36	13,44	26,81	13,36	26,65
	<i>Cuon alpinus</i>	14,30	22,06	16,13	21,82	13,49	24,89	15,68	22,98
Fossil North Sea	667	19,82	20,38	-	-	19,32	19,88	-	-
	1683	27,98	28,54	-	-	30,57	31,13	-	-
	2103	20,63	21,19	-	-	22,43	22,99	-	-
	2104	22,36	22,92	-	-	22,53	23,09	-	-
	2196	28,62	29,18	-	-	30,60	31,16	-	-
	2329	24,44	25,00	-	-	26,17	26,73	-	-
	2620	29,38	29,94	-	-	32,05	32,61	-	-
	3219	21,11	21,67	-	-	21,91	22,47	-	-
	3293	24,65	25,21	-	-	26,04	26,60	-	-
NMR89	-	-	-	-	18,36	18,92	-	-	

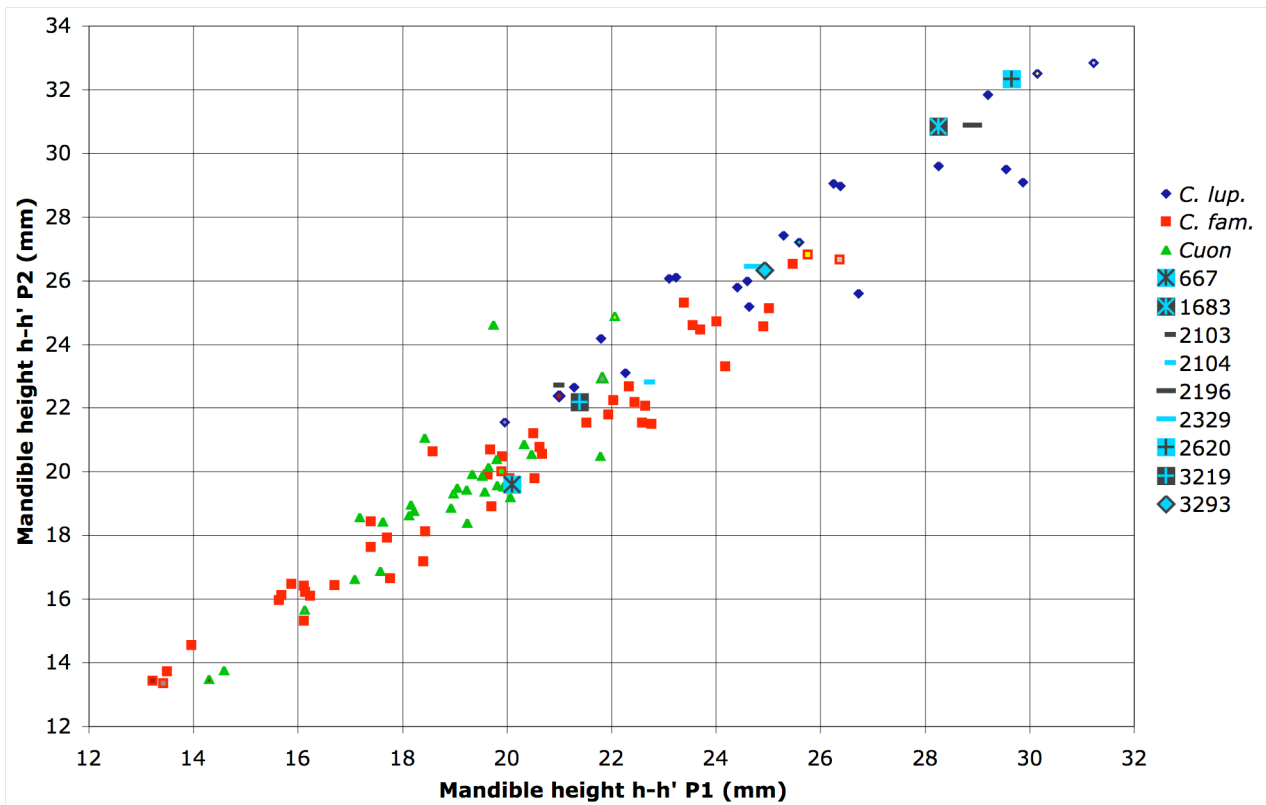


Figure 4.14: Scatter plot of parameters 'Mandible height  $h-h'$ '  $P_1$  vs.  $P_2$  for the fossil North Sea specimens and the comparative material (in mm). Legend, see tables 4.1 and 4.2.

## 4.2.3 Mandible height $h-h'$ under $P_3$ and $P_4$

### 4.2.3.1 Results comparative material

For all values mentioned below see both table 4.18 and fig. 4.15 unless stated otherwise.

**x** For both parameters *C. l. lupus* has on average the largest mandible height under  $P_3$  and  $P_4$  (fig. IV.1) while both *C. l. familiaris* and *Cuon alpinus* have significantly smaller heights and lie closer together (table 4.18).

**SD vs. n** Standard deviations of both *Canis* species lie very close together for these two parameters (*C. l. familiaris* has a SD of 3.31 mm for  $h-h'$   $P_3$  and *C. l. lupus* of 3.30 mm), while the sample size of *C. l. familiaris* is more than twice as large as that of *C. l. lupus* (n of respectively 42 and 18) (table 4.18). Variation in *Cuon alpinus* is much smaller than in *Canis* (SD of 2.06 for  $h-h'$   $P_3$ ), while the sample size of this species (n 27) is not. Values are similar for parameter  $h-h'$   $P_4$ .

**Sample ranges:** see table 4.18. The sample ranges of *Cuon alpinus* and *C. l. lupus* overlap significantly with each other and *C. l. familiaris* shows much overlap with these both species. In the lower parts of fig. 4.15 both *C. l. familiaris* and *Cuon alpinus* are present and only the uppermost parts of the figure are occupied by only one species: *C. l. lupus*. Sample ranges of *Cuon alpinus* and *C. l. familiaris* are very similar in size and in minima and maxima. Also for these parameters there is a distinction within the *C. l. familiaris* group, separating the fossil specimens from the Netherlands from the recent specimens from Suriname. As was the trend for previous parameters recent specimens from Suriname plot over the entire *C. l. familiaris* range, although the *C. l. familiaris* specimens with the smallest heights are all recent specimens from Suriname (fig. VII.6). The fossil specimens from the Netherlands plot more in the upper *C. l. familiaris* range. Data points of *C. l. familiaris* plot evenly over its range in a quite linear way, but in the *Cuon alpinus* and *C. l. lupus* data clouds there are some deviating specimens (fig. 4.15). Most *Cuon alpinus* specimens are concentrated in the lower part of fig. 4.15 (below approximately coordinates 23, 23 mm) and only one specimen plots far into the *C. l. lupus* range (specimen 945, approximate coordinate 27, 27 mm). *C. l. lupus* specimens 445834 and *lupus-g* deviate a little from the rest of the *C. l. lupus* specimens. There are no remarkable *C. l. familiaris* specimens.

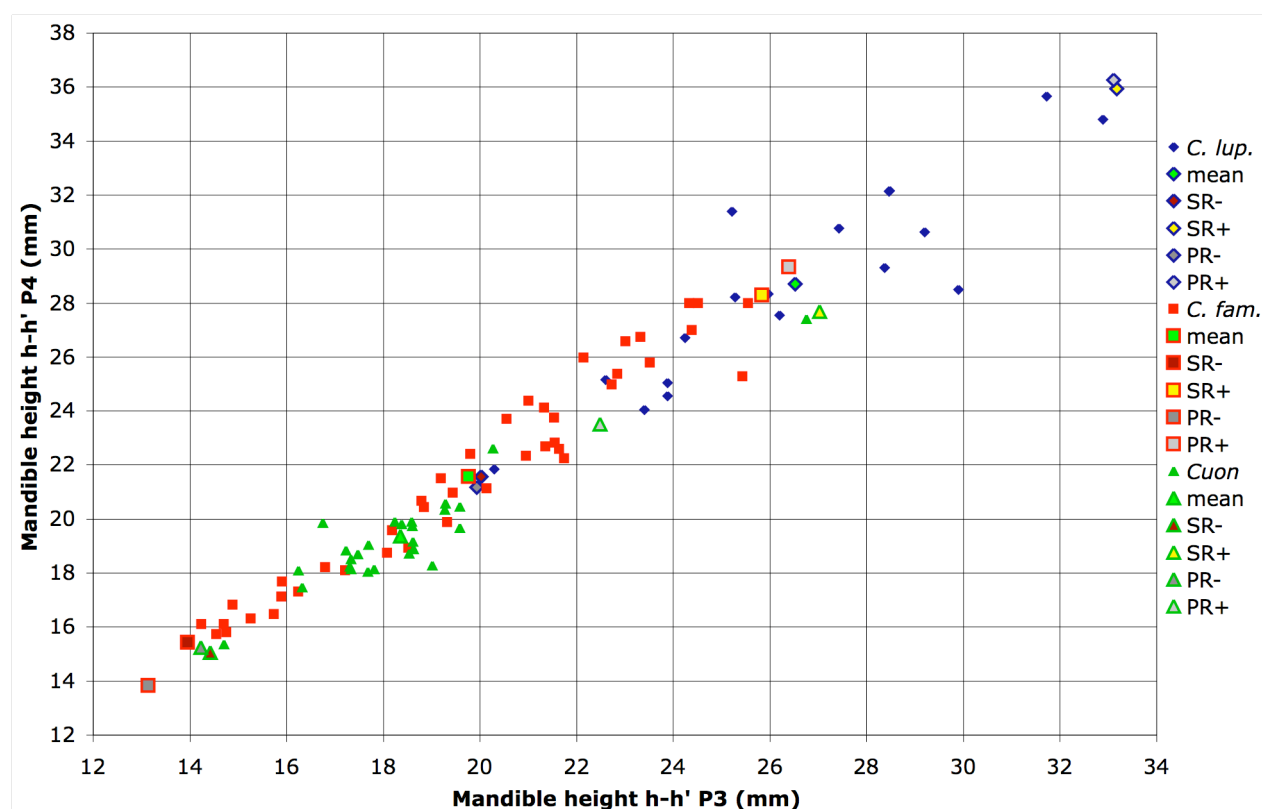
**Population ranges:** see table 4.18. For the population ranges there is still some overlap between the *Cuon alpinus* and *C. l. lupus* ranges. *C. l. familiaris* overlaps significantly with these both species, plotting from lower than the *Cuon alpinus* minimum to close to the *C. l. lupus* mean (fig. 4.15).

**Trend lines** Parameters  $h-h'$   $P_3$  and  $h-h'$   $P_4$  are very similar and as a result the data clouds of the three comparative species plot quite linearly in fig. 4.15. The *Canis* trend lines (if plotted) are a continuation of each other and the *Cuon alpinus* trend line plots quite close to these trend lines. There are no major

differences between the comparative species with respect to their  $h-h'$  P<sub>3</sub> and P<sub>4</sub> values: all three comparative species have comparable  $h-h'$  P<sub>3</sub> values in proportion to their  $h-h'$  P<sub>4</sub> values. For this reason, a figure including trend lines is not given; trend lines would not be helpful in the determination of the identity of the fossil North Sea specimens.

**Table 4.18: Statistics of the parameters 'Mandible height  $h-h'$ ' P<sub>3</sub> (left) and P<sub>4</sub> (right) of the comparative material (in mm).** Legend: see table 4.1.

Statistics	Mandible height $h-h'$ P <sub>3</sub>			Mandible height $h-h'$ P <sub>4</sub>		
	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>
Sample size (n)	18	42	27	18	42	27
Sample mean ( $\bar{x}$ )	26,52	19,76	18,35	28,71	21,58	19,38
Standard deviation (SD)	3,30	3,31	2,06	3,77	3,87	2,07
Minimum (MIN)	20,30	14,24	14,70	21,85	15,72	15,35
Maximum (MAX)	32,89	25,55	26,75	35,65	28,00	27,41
Sample range MIN	20,02	13,96	14,42	21,57	15,44	15,07
Sample range MAX	33,17	25,83	27,03	35,93	28,28	27,69
Population range MIN	19,93	13,14	14,23	21,17	13,83	15,25
Population range MAX	33,11	26,38	22,48	36,26	29,33	23,51



**Figure 4.15: Scatter plot of parameters 'Mandible height  $h-h'$ ' P<sub>3</sub> vs. P<sub>4</sub> for the comparative material (in mm).** Legend, see table 4.1.

#### 4.2.3.2 Results fossil North Sea material

Not all 13 fossil North Sea specimens had values for both parameters, thus only 9 specimens could be plotted in fig. 4.16.

##### Specimens 534, 535 and NMR90

These three specimens miss a large anterior part of their hemimandible, thus no data is available for parameters  $h-h'$  P<sub>3</sub> and P<sub>4</sub> for 534, 535 and NMR90 (appendix I).

### **Specimen 667**

Specimen 667 falls entirely within the sample and population ranges of *C. I. familiaris* (fossil part) and *Cuon alpinus* for both parameters (table 4.19, fig. 4.16 and fig. VII.6). The specimen ranges falls entirely outside (below) the *C. I. lupus* sample range for parameter  $h-h'$   $P_4$  and both sample and population ranges for parameter  $h-h'$   $P_3$ . Overlap with the *C. I. lupus* population range of parameter  $h-h'$   $P_4$  is only partial: 667 partially falls below this range. The mean value of 667 for parameter  $h-h'$   $P_3$  (19.22 mm) is very similar to the average *C. I. familiaris* specimen (with a distance of 0.54 mm between the two mean values), slightly less similar to the average *Cuon alpinus* specimen (0.87 mm) and most dissimilar to the average *C. I. lupus* specimen (7.30 mm) (appendix XIII). Values are similar for parameter  $h-h'$   $P_4$ .

### **Specimen 1683**

Specimen 1683 falls entirely outside (above) the sample and population ranges of *C. I. familiaris* and *Cuon alpinus* and entirely within the *C. I. lupus* sample and population ranges for both parameters (table 4.19). Specimen 1683 plots in the upper part of fig. 4.16 and is most similar to the average *C. I. lupus* specimen (with a distance of 3.03 mm between the two mean values for parameter  $h-h'$   $P_3$ ) and much less similar to the average *C. I. familiaris* and *Cuon alpinus* specimens (with respectively 9.79 and 11.20 mm) (appendix XIII). This trend is the same for parameter  $h-h'$   $P_4$ .

### **Specimen 2103**

For both parameters specimen 2103 falls entirely within the *C. I. lupus* and *C. I. familiaris* (fossil part) sample and population ranges, within the *Cuon alpinus* sample ranges and outside (above) the *Cuon alpinus* population ranges (table 4.19, fig. 4.16 and fig. VII.6). The mean value of 2103 for parameter  $h-h'$   $P_3$  (23.03 mm) is most similar to the average *C. I. familiaris* specimen (with a distance of 3.27 mm between the two mean values), less similar to the average *C. I. lupus* specimen (with 3.49 mm) and more dissimilar to the average *Cuon alpinus* specimen (4.68 mm) (appendix XIII). Values are similar for parameter  $h-h'$   $P_4$ , but the trend is slightly reversed: 2103 also for this parameter is most dissimilar to *Cuon alpinus*, but more similar to *C. I. lupus* than to *C. I. familiaris*.

### **Specimen 2104**

Specimen 2104 falls entirely within the sample and population ranges of both *Canis* species (fossil part of the *C. I. familiaris* sample range) and within the sample ranges of *Cuon alpinus* for both parameters (table 4.19, fig. 4.16 and fig. VII.6). It partly falls outside (above) the *Cuon alpinus* population range for parameter  $h-h'$   $P_4$  and entirely outside (above) the *Cuon alpinus* population range for  $h-h'$   $P_4$ . The mean value of 2104 for parameter  $h-h'$   $P_3$  (22.26 mm) is most similar to the average *C. I. familiaris* specimen (with a distance of 2.50 mm between the two mean values), less similar to the average *Cuon alpinus* (with 3.91 mm) and most dissimilar to the average *C. I. lupus* (with 4.26 mm) (appendix XIII). Since parameters  $h-h'$   $P_3$  and  $h-h'$   $P_4$  are very similar, the mean values of  $h-h'$   $P_4$  are comparable, but the trend is partly reversed: specimen 2104 is still most similar to the average *C. I. familiaris* specimen, but more similar to the average *C. I. lupus* than *Cuon alpinus* specimen.

### **Specimen 2196**

Specimen 2196 falls entirely outside (above) the *C. I. familiaris* and *Cuon alpinus* sample and population ranges and entirely within the *C. I. lupus* sample and population ranges for both parameters (table 4.19). As is already obvious from fig. 4.16, specimen 2196 is most similar to the average *C. I. lupus* specimen (with a distance of 3.48 mm between the two mean values for parameter  $h-h'$   $P_3$ ) and much more dissimilar to the average *C. I. familiaris* and *Cuon alpinus* specimens (respectively 10.24 and 11.65 mm). The values and trend are similar for parameter  $h-h'$   $P_4$  (appendix XIII).

### **Specimen 2329**

Specimen 2329 falls entirely within the *C. I. lupus* sample and population ranges for both parameters (table 4.19). It falls entirely outside (above) the sample and population ranges of *C. I. familiaris* and *Cuon alpinus* for parameter  $h-h'$   $P_4$ . For parameter  $h-h'$   $P_3$  specimen 2329 falls outside (above) the *C. I. familiaris* sample range and partly outside (above) that population range, inside the *Cuon alpinus* sample range and entirely outside (above) the *Cuon alpinus* population range. The mean value of 2329 for parameter  $h-h'$   $P_3$  (26.46 mm) is very similar to the average *C. I. lupus* specimen (with a distance of 0.06 mm between the two mean values) and much more dissimilar to the average *C. I. familiaris* and *Cuon alpinus* specimens (respectively 6.70 and 8.11 mm) (fig. 4.16 and appendix XIII). The values and trend are similar for parameter  $h-h'$   $P_4$ .

### **Specimen 2620**

This fossil North Sea specimen misses the lowermost part of the body of the hemimandible starting below  $P_4$  towards distal (appendix I). It only has values for  $h-h'$   $P_3$  and as a consequence could not be plotted in fig. 4.16. Specimen 2620 falls entirely within the sample and population ranges of *C. I. lupus* and entirely outside (above) the *C. I. familiaris* and *Cuon alpinus* sample and population ranges (table 4.19). The mean value of



2620 for parameter  $h-h'$  P<sub>3</sub> (29.87 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 3.35 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (respectively 10.11 and 11.52 mm) (appendix XIII).

### Specimen 3219

Specimen 3219 falls entirely within the sample and population ranges of both *Canis* species (fossil part of the *C. l. familiaris* sample range) and within the sample ranges of *Cuon alpinus* for both parameters (table 4.19, fig. 4.16 and fig. VII.6). It falls partly outside (above) the *Cuon alpinus* population range for parameter  $h-h'$  P<sub>3</sub> and entirely outside (above) the *Cuon alpinus* population range for parameter  $h-h'$  P<sub>4</sub>. The mean value of 3219 for parameter  $h-h'$  P<sub>3</sub> (22.32 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 2.56 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 3.97 mm) and most dissimilar to the average *C. l. lupus* specimen (with 4.20 mm) (appendix XIII). Values for parameter  $h-h'$  P<sub>4</sub> are of the same order of magnitude, but for this parameter specimen 3219 is, after *C. l. familiaris*, most similar to *C. l. lupus* instead of *Cuon alpinus*.

### Specimen 3293

Specimen 3293 falls entirely within the sample and population ranges of *C. l. lupus* for both parameters, within the sample and population range of *C. l. familiaris* for parameter  $h-h'$  P<sub>3</sub> and within the sample range of *Cuon alpinus* for this parameter (table 4.19 and fig. 4.16). Specimen 3293 falls entirely outside (above) the sample ranges of *C. l. familiaris* and *Cuon alpinus* for parameter  $h-h'$  P<sub>4</sub> and outside (above) the *Cuon alpinus* population ranges for both parameters. Finally, 3293 partly falls outside (above) the *C. l. familiaris* population range for  $h-h'$  P<sub>4</sub>. The mean value of 3293 for parameter  $h-h'$  P<sub>3</sub> (25.40 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 1.12 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (respectively 5.64 and 7.05 mm) (appendix XIII). This trend is the same for parameter  $h-h'$  P<sub>4</sub>.

### Specimen NMR89

Specimen NMR89 only partly overlaps with the lower part of the *C. l. lupus* sample and population ranges for parameter  $h-h'$  P<sub>3</sub> and falls entirely outside (below) the *C. l. lupus* sample and population ranges for parameter  $h-h'$  P<sub>4</sub> (table 4.19 and fig. 4.16). NMR89 falls entirely within all remaining ranges (fossil part of the *C. l. familiaris* sample range, fig. VII.6). The mean value of NMR89 for parameter  $h-h'$  P<sub>3</sub> (19.91 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.15 mm between the two mean values), slightly less similar to the average *Cuon alpinus* specimen (with 1.56 mm) and much more dissimilar to the average *C. l. lupus* specimen (with 6.61 mm) (appendix XIII). This trend is partly reversed for parameter  $h-h'$  P<sub>4</sub>: for this parameter NMR89 is most similar to the average *Cuon alpinus* specimen (with 0.35 mm), less similar to the average *C. l. familiaris* specimen (with 1.85 mm) and also most dissimilar to the average *C. l. lupus* specimen (with 8.98 mm).

**Table 4.19: Comparison of the specimen ranges of the fossil North Sea specimens with the sample and population ranges of the comparative material for parameters 'Mandible height  $h-h'$ ' P<sub>3</sub> (left) and P<sub>4</sub> (right) (in mm). Sample and population ranges of the comparative material are as given in table 4.18. Specimen ranges were calculated as explained in table 4.2.**

Canidae material		Mandible height $h-h'$ P <sub>3</sub>				Mandible height $h-h'$ P <sub>4</sub>			
		- Sample range +		- Population range +		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	20,02	33,17	19,93	33,11	21,57	35,93	21,17	36,26
	<i>C. l. familiaris</i>	13,96	25,83	13,14	26,38	15,44	28,28	13,83	29,33
	<i>Cuon alpinus</i>	14,42	27,03	14,23	22,48	15,07	27,69	15,25	23,51
Fossil North Sea	667	18,94	19,50	-	-	20,74	21,30	-	-
	1683	29,27	29,83	-	-	35,04	35,60	-	-
	2103	22,75	23,31	-	-	25,39	25,95	-	-
	2104	21,98	22,54	-	-	24,33	24,89	-	-
	2196	29,72	30,28	-	-	32,16	32,72	-	-
	2329	26,18	26,74	-	-	29,70	30,26	-	-
	2620	29,59	30,15	-	-	-	-	-	-
	3219	22,04	22,60	-	-	24,39	24,95	-	-
	3293	25,12	25,68	-	-	28,95	29,51	-	-
	NMR89	19,63	20,19	-	-	19,45	20,01	-	-

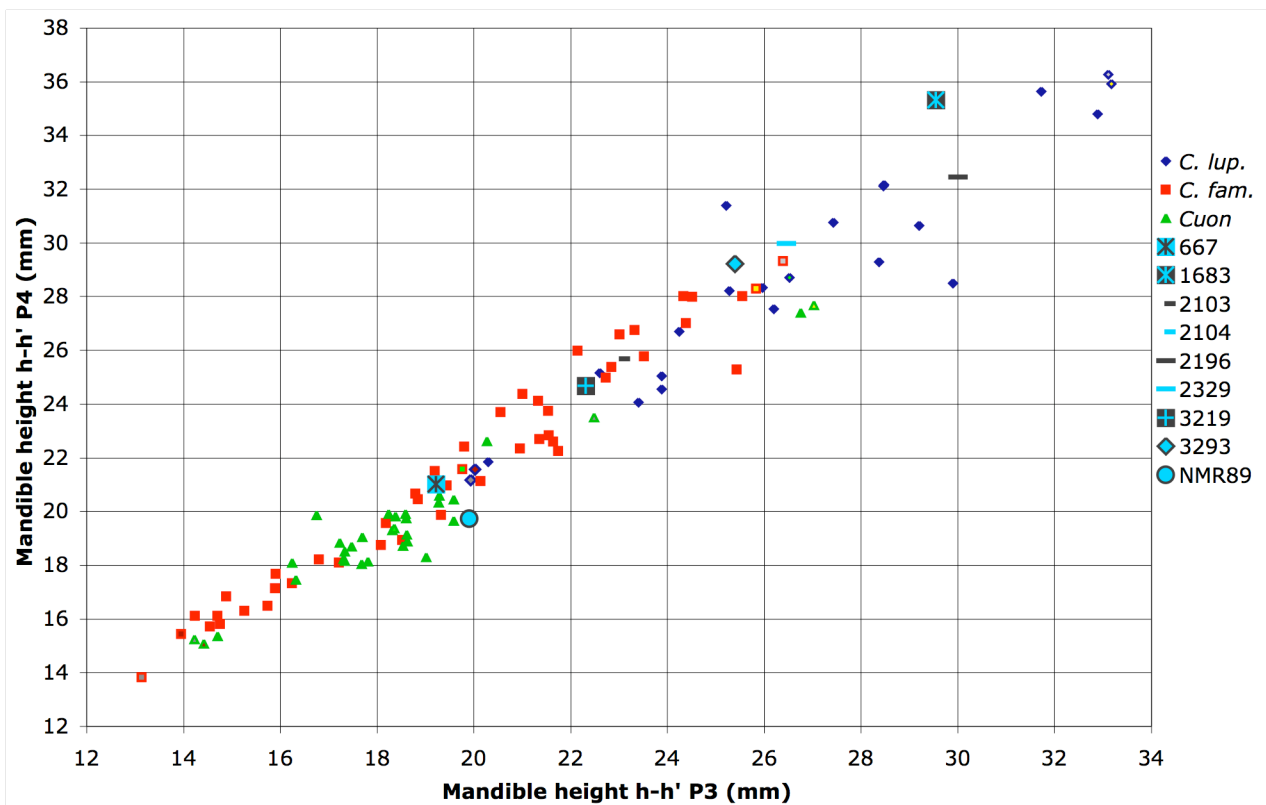


Figure 4.16: Scatter plot of parameters 'Mandible height  $h-h'$ ' P<sub>3</sub> vs. P<sub>4</sub> for the fossil North Sea specimens and the comparative material (in mm). Legend, see tables 4.1 and 4.2.

## 4.2.4 Mandible height $h-h'$ under M<sub>1</sub> and M<sub>2</sub>

### 4.2.4.1 Results comparative material

For all values see both table 4.20 and fig. 4.17 unless stated otherwise.

**x** For both parameters *C. l. lupus* has on average the largest mandible height under M<sub>1</sub> and M<sub>2</sub> (fig. IV.1), while both *C. l. familiaris* and *Cuon alpinus* have significantly smaller heights and lie closer together (table 4.20).

**SD vs. n** *C. l. familiaris* shows the greatest variation in mandible heights below its molars (SD of 4.22 mm for  $h-h'$  M<sub>1</sub>), but *C. l. lupus* shows an almost equal amount of variation (SD of 4.18 mm for  $h-h'$  M<sub>1</sub>), although the sample size of this species is significantly smaller than that of *C. l. familiaris*. The variation in *Cuon alpinus* mandibles heights is much smaller than in *Canis* (SD of 1.17 mm for  $h-h'$  M<sub>1</sub>), although the sample size is relatively large (table 4.20). This trend is the same for parameter  $h-h'$  M<sub>2</sub>.

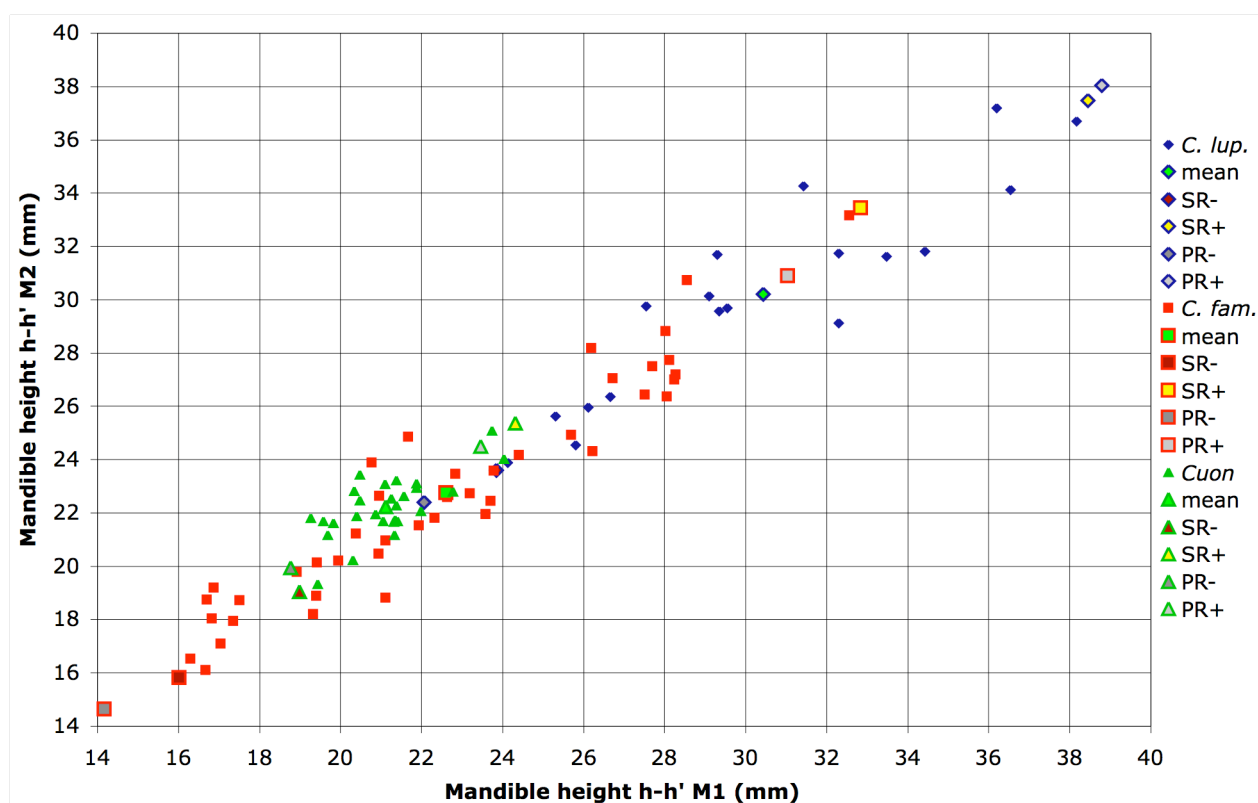
**Sample ranges:** see table 4.20. *Cuon alpinus* has a quite small range and plots in a concentrated data cloud in the lower part of fig. 4.17. Both *Canis* species have much larger ranges: the lowest *C. l. lupus* values partly overlap with the upper *Cuon alpinus* range and the maximum value form the uppermost part of the figure, while *C. l. familiaris* overlaps significantly with both *Cuon alpinus* and *C. l. lupus*. Also for these parameters there is a slight distinction within the *C. l. familiaris* group, separating the fossil specimens from the Netherlands from the recent specimens from Suriname. Most specimens of the two subgroups have similar average mandible heights below their molars, although the *C. l. familiaris* specimens with the smallest heights are recent specimens from Suriname and the *C. l. familiaris* specimens with the largest heights are fossil specimens from the Netherlands (fig. VII.7). Data points (specimens) of all three comparative species are quite evenly distributed along their ranges and there are no remarkable specimens that deviate much from this linear band of data points (fig. 4.17).

**Population ranges:** see table 4.20. For the population ranges there is still some overlap between the *Cuon alpinus* and *C. l. lupus* ranges. *C. l. familiaris* overlaps significantly with these both species, plotting from lower than the *Cuon alpinus* minimum to larger than the *C. l. lupus* mean in fig. 4.17.

**Trend lines** Parameters  $h-h'$  M<sub>1</sub> and  $h-h'$  M<sub>2</sub> are very similar and as a result the data clouds of the three comparative species plot quite linearly in fig. 4.17. There are no significant differences between the three comparative species with respect to  $h-h'$  M<sub>1</sub> in proportion  $h-h'$  M<sub>2</sub>. Trend lines are thus not helpful in the determination of the identity of the fossil North Sea specimens and will not be plotted or discussed.

**Table 4.20: Statistics of the parameters ‘Mandible height  $h-h'$ ’  $M_1$  (left) and  $M_2$  (right) of the comparative material (in mm).** Legend: see table 4.1.

Statistics	Mandible height $h-h'$ $M_1$			Mandible height $h-h'$ $M_2$		
	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>
Sample size (n)	18	42	27	18	42	27
Sample mean ( $\bar{x}$ )	30,43	22,61	21,11	30,21	22,76	22,23
Standard deviation (SD)	4,18	4,22	1,17	3,91	4,06	1,14
Minimum (MIN)	24,13	16,30	19,26	23,88	16,09	19,34
Maximum (MAX)	38,17	32,56	24,04	37,19	33,15	25,10
Sample range MIN	23,85	16,02	18,98	23,60	15,81	19,06
Sample range MAX	38,45	32,84	24,32	37,47	33,43	25,38
Population range MIN	22,06	14,17	18,77	22,39	14,63	19,95
Population range MAX	38,79	31,05	23,45	38,03	30,89	24,51



**Figure 4.17: Scatter plot of parameters ‘Mandible height  $h-h'$ ’  $M_1$  vs.  $M_2$  for the comparative material (in mm).** Legend, see table 4.1.

#### 4.2.4.2 Results fossil North Sea material

Not all 13 fossil North Sea specimens had values for both parameters, thus only 10 specimens could be plotted in fig. 4.18.

##### Specimen 534

This fossil North Sea specimen misses a large anterior part of its hemimandible (appendix I), thus data are only present for parameter  $h-h'$   $M_2$  and 534 could not be plotted in fig. 4.18. For this parameter specimen 534 falls entirely within the sample and population ranges of *C. l. lupus* and entirely outside (above) the *Cuon alpinus* sample and population ranges (table 4.21). This specimen also falls entirely outside (above) the *C. l. familiaris* population range, but only partly outside the sample range of this species. The mean value of 534 for parameter  $h-h'$   $M_2$  (33.32 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 3.11 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 10.56 and 11.09 mm respectively) (appendix XIII).

### **Specimen 535**

For both parameters specimen 535 falls entirely within the sample and population ranges of both *Canis* species and entirely outside (above) the *Cuon alpinus* sample and population ranges (table 4.21 and fig. 4.18). The mean value of 535 for parameter  $h-h'$   $M_1$  (29.85 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.58 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 7.24 and 8.74 mm respectively) (appendix XIII). This trend of mean values is the same for parameter  $h-h'$   $M_2$ .

### **Specimen 667**

Specimen 667 falls outside (below) the *C. l. lupus* sample range for parameter  $h-h'$   $M_1$ , but inside corresponding population range (table 4.21 and fig. 4.18). This specimen also falls within the sample and population ranges of *C. l. lupus* for parameter  $h-h'$   $M_2$  and within the *C. l. familiaris* sample and population ranges (fossil part, fig. VII.7) for both parameters. 667 Falls slightly outside (above) the *Cuon alpinus* population range for parameter  $h-h'$   $M_1$  and entirely outside the *Cuon alpinus* population range for parameter  $h-h'$   $M_2$ . Finally, 667 falls entirely within the *Cuon alpinus* sample ranges for both parameters. The mean value of 667 for parameter  $h-h'$   $M_1$  (23.21 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.60 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 2.10 mm) and most dissimilar to the average *C. l. lupus* specimen (with 7.22 mm) (appendix XIII). This trend is the same for parameter  $h-h'$   $M_2$ .

### **Specimen 1683**

Specimen 1683 falls entirely within the *C. l. lupus* sample and population ranges and entirely outside (above) the *C. l. familiaris* and *Cuon alpinus* sample and population ranges for both parameters (table 4.21 and fig. 4.18). The mean value of 1683 for parameter  $h-h'$   $M_1$  (36.04 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 5.61 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 13.43 and 14.93 mm respectively) (appendix XIII). This trend of mean values is the same for parameter  $h-h'$   $M_2$ .

### **Specimen 2103**

Specimen 2103 falls entirely within the sample and population ranges of both *Canis* species and entirely outside (above) the *Cuon alpinus* sample and population ranges for both parameters (table 4.21 and fig. 4.18). The mean value of 2103 for parameter  $h-h'$   $M_1$  (26.35 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 3.74 mm between the two mean values), slightly less similar to the average *C. l. lupus* specimen (with 4.08 mm) and most dissimilar to the average *Cuon alpinus* specimen (with 5.24 mm) (appendix XIII). This trend is partly reversed for parameter  $h-h'$   $M_2$ : 2103 is still most dissimilar to *Cuon alpinus*, but slightly more similar to the average *C. l. lupus* than to the *C. l. familiaris* specimen.

### **Specimen 2104**

The specimen range of 2104 partly falls outside (below) the sample range of *C. l. lupus* for parameter  $h-h'$   $M_1$  and partly outside (above) the *Cuon alpinus* population range for parameter  $h-h'$   $M_2$  (table 4.21 and fig. 4.18). Specimen 2104 falls entirely within the *C. l. lupus* population range for parameter  $h-h'$   $M_1$ , the *C. l. familiaris* sample and population ranges for parameter  $h-h'$   $M_1$  (fossil part, fig. VII.7), both *Canis* sample and population ranges for parameter  $h-h'$   $M_2$  and the *Cuon alpinus* sample ranges for both parameters. Specimen 2104 falls entirely outside (above) the *Cuon alpinus* population range for parameter  $h-h'$   $M_1$ . The mean value of 2104 for parameter  $h-h'$   $M_1$  (24.02 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 1.41 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 2.91 mm) and most dissimilar to the average *C. l. lupus* specimen (with 6.41 mm) (appendix XIII). This trend is the same for parameter  $h-h'$   $M_2$ .

### **Specimen 2196**

Specimen 2196 falls entirely within the *C. l. lupus* sample and population ranges and entirely outside (above) the *Cuon alpinus* sample and population range for both parameters (table 4.21 and fig. 4.18). This specimen also falls entirely outside (above) the *C. l. familiaris* sample and population ranges for parameter  $h-h'$   $M_1$  and the *C. l. familiaris* population range for parameter  $h-h'$   $M_2$ . Specimen 2196 falls inside the sample range of *C. l. familiaris* for parameter  $h-h'$   $M_2$ . The mean value of 2196 for parameter  $h-h'$   $M_1$  (33.58 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 3.15 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with respectively 10.97 and 12.47 mm) (appendix XIII). This trend is the same for parameter  $h-h'$   $M_2$ .

**Specimen 2329**

Specimen 2329 falls entirely within the *C. l. lupus* sample and population ranges and entirely outside (above) the *Cuon alpinus* sample and population range for both parameters (table 4.21 and fig. 4.18). This specimen also falls entirely outside (above) the *C. l. familiaris* population range for parameter  $h-h'$  M<sub>1</sub> and partly outside (above) the *C. l. familiaris* population range for parameter  $h-h'$  M<sub>2</sub>. Specimen 2329 falls entirely within the *C. l. familiaris* sample ranges for both parameters. The mean value of 2329 for parameter  $h-h'$  M<sub>1</sub> (31.35 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 1.02 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with respectively 8.84 and 10.34 mm) (appendix XIII). This trend is the same for parameter  $h-h'$  M<sub>2</sub>.

**Specimens 2620 and NMR90**

These two specimens miss a substantial part of the body of the hemimandible below their (pre)molars, thus parameters  $h-h'$  M<sub>1</sub> and  $h-h'$  M<sub>2</sub> could not be taken (appendix I).

**Specimen 3219**

Specimen 3219 falls entirely within the sample and population range of both *Canis* species for both parameters (fossil part of the *C. l. familiaris* sample range, fig. VII.7) and entirely outside (above) the *Cuon alpinus* sample and population ranges for parameter  $h-h'$  M<sub>1</sub> (table 4.21 and fig. 4.18). This specimen partly falls within the *Cuon alpinus* sample range for parameter  $h-h'$  M<sub>2</sub> and entirely outside (above) the corresponding population range. The mean value of 3219 for parameter  $h-h'$  M<sub>1</sub> (25.27 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 2.66 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 4.16 mm) and most dissimilar to the average *C. l. lupus* specimen (with 5.16 mm) (appendix XIII). This trend is the same for parameter  $h-h'$  M<sub>2</sub>.

**Specimen 3293**

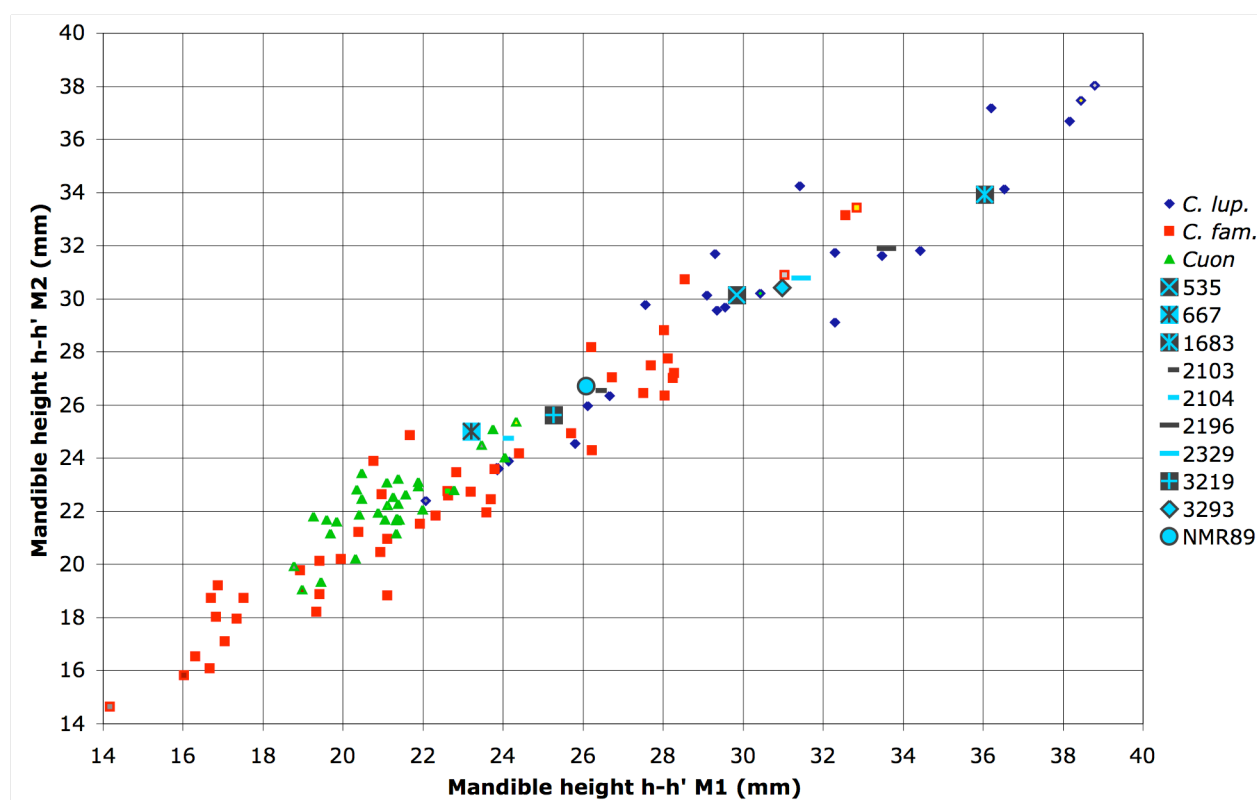
Specimen 3293 falls entirely within the *C. l. lupus* sample and population ranges and entirely outside (above) the *Cuon alpinus* sample and population range for both parameters (table 4.21 and fig. 4.18). It also falls entirely within the *C. l. familiaris* sample and population ranges for parameter  $h-h'$  M<sub>2</sub>, within the *C. l. familiaris* sample range for  $h-h'$  M<sub>1</sub> and partly outside (above) corresponding population range. The mean value of 3293 for parameter  $h-h'$  M<sub>1</sub> (30.97 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.54 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 8.36 and 9.86 mm respectively) (appendix XIII). This trend is the same for parameter  $h-h'$  M<sub>2</sub>.

**Specimen NMR89**

NMR89 falls entirely within the sample and population range of both *Canis* species (fossil part of the *C. l. familiaris* sample range, fig. VII.7) and entirely outside (above) the *Cuon alpinus* sample and population ranges for both parameters (table 4.21 and fig. 4.18). The mean value of NMR89 for parameter  $h-h'$  M<sub>1</sub> (26.08 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 4.35 mm between the two mean values), less similar to the average *C. l. lupus* specimen (with 3.47 mm) and most dissimilar to the average *Cuon alpinus* specimen (with 4.97 mm) (appendix XIII). This trend is partly reversed for parameter  $h-h'$  M<sub>2</sub>: NMR89 is still most dissimilar to *Cuon alpinus*, but slightly more similar to the average *C. l. lupus* than to the *C. l. familiaris* specimen.

**Table 4.21: Comparison of the specimen ranges of the fossil North Sea specimens with the sample and population ranges of the comparative material for parameters ‘Mandible height  $h-h'$ ’  $M_1$  (left) and  $M_2$  (right) (in mm). Sample and population ranges of the comparative material are as given in table 4.20. Specimen ranges were calculated as explained in table 4.2.**

Canidae material		Mandible height $h-h'$ $M_1$				Mandible height $h-h'$ $M_2$			
		- Sample range +		- Population range +		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	23,85	38,45	22,06	38,79	23,60	37,47	22,39	38,03
	<i>C. l. familiaris</i>	16,02	32,84	14,17	31,05	15,81	33,43	14,63	30,89
	<i>Cuon alpinus</i>	18,98	24,32	18,77	23,45	19,06	25,38	19,95	24,51
Fossil North Sea	534	-	-	-	-	33,04	33,60	-	-
	535	29,57	30,13	-	-	29,86	30,42	-	-
	667	22,93	23,49	-	-	24,73	25,29	-	-
	1683	35,76	36,32	-	-	33,65	34,21	-	-
	2103	26,07	26,63	-	-	26,27	26,83	-	-
	2104	23,74	24,30	-	-	24,45	25,01	-	-
	2196	33,30	33,86	-	-	31,61	32,17	-	-
	2329	31,17	31,73	-	-	30,50	31,06	-	-
	3219	24,99	25,55	-	-	25,33	25,89	-	-
	3293	30,69	31,25	-	-	30,15	30,71	-	-
	NMR89	25,80	26,36	-	-	26,42	26,98	-	-



**Figure 4.18: Scatter plot of parameters ‘Mandible height  $h-h'$ ’  $M_1$  vs.  $M_2$  for the fossil North Sea specimens and the comparative material (in mm). Legend, see tables 4.1 and 4.2.**

### Values from literature

‘Mandible height  $h-h'$ ’  $M_1$ ’ is the third parameter for which values of comparative *Cuon alpinus* specimens were found in literature (Adam (1959) and Pérez Ripoll et al. (2010)). Values of eleven specimens were added to the comparative *Cuon alpinus* dataset (which resulted in a sample size of 38 instead of 27) and new statistics were calculated (appendix IX). The fossil North Sea specimens were compared to the new ranges and following results were obtained (see also appendix XII):

For specimens 1683, 2196, 2329 and 3293 previous results are confirmed by the new extended dataset: these specimens still fall entirely outside the *Cuon alpinus* sample and population ranges (appendix IX). For all remaining specimens results are different. Specimen 535 originally fell entirely outside the *Cuon alpinus* sample and population ranges and still falls entirely outside the new population range, but falls partly within the new sample range. Specimens 667 and 2104 both fell originally within the sample range of *Cuon alpinus* and partly outside the corresponding population range, but fall entirely within both *Cuon alpinus* ranges for the extended dataset. Specimens 2103, 3219 and NMR89 originally fell outside both *Cuon alpinus* ranges, but fall entirely within the *Cuon alpinus* sample and population ranges for the new dataset.

## 4.2.5 Ratios of mandibular length, width and height

According to observations from Pérez Ripoll et al. (2010) the length, width and height of *Cuon alpinus* mandibles are reduced with respect to *C. l. lupus*, but not in the same amount: “If we compare the average alveolar  $P_1-M_2$  length between the *C. alpinus* and the *C. l. lupus*, we find that the length is 18% shorter in the *Cuon* than in the *Canis*, whereas this ratio is reduced to 10% when calculated by taking the mandibular thickness between  $P_4-M_1$  and to 4% when calculated taking the height between  $P_2-P_3$ .” (Pérez Ripoll et al., 2010). This means that the length, width and height of the *Cuon alpinus* mandible is smaller than that of *C. l. lupus*, but that in *Cuon alpinus* the thickness of the mandible is relatively less reduced in size than the length compared to *C. l. lupus*. The height of the *Cuon alpinus* mandible is least reduced in size relative to the length (compared to *C. l. lupus*). Due to these different amounts of reduction in mandible size *Cuon alpinus* mandibles are shorter but sturdier than *C. l. lupus* mandibles. Although the quantification of Pérez Ripoll et al. (2010) only concerned the comparison of one *Cuon alpinus* specimen with one *C. l. lupus* specimen, this conclusion generally holds true for all *Cuons*, because these different mandible ratios of *Cuon alpinus* and *C. l. lupus* were also observed in all comparative specimens that were used for this study and in the fossil North Sea specimens (4.1.1.2). These ratios will be quantified in this section. For *C. l. familiaris* and *Cuon alpinus* was calculated how much the length, width and height of the mandible of an average specimen (x value) is reduced in proportion to the average *C. l. lupus* specimen (x value), which is taken as reference value. The three parameters that were used to represent mandibular length, width and height (that are most similar to the parameters used by Pérez Ripoll et al. (2010)), are: Alveolar length  $P_1-M_2$ , Width of the mandible  $i-i'$  and Height  $h-h'$   $P_3$ . Since mandible length, width and height were already quantitatively compared in previous sections (4.1.2, 4.2.1 and 4.2.3), the aim of this section is not to compare the individual percentages or the amount of reduction, but to observe and compare a possible trend in fragility of *Cuon alpinus* and *Canis* mandibles.

### 4.2.5.1 Results comparative material

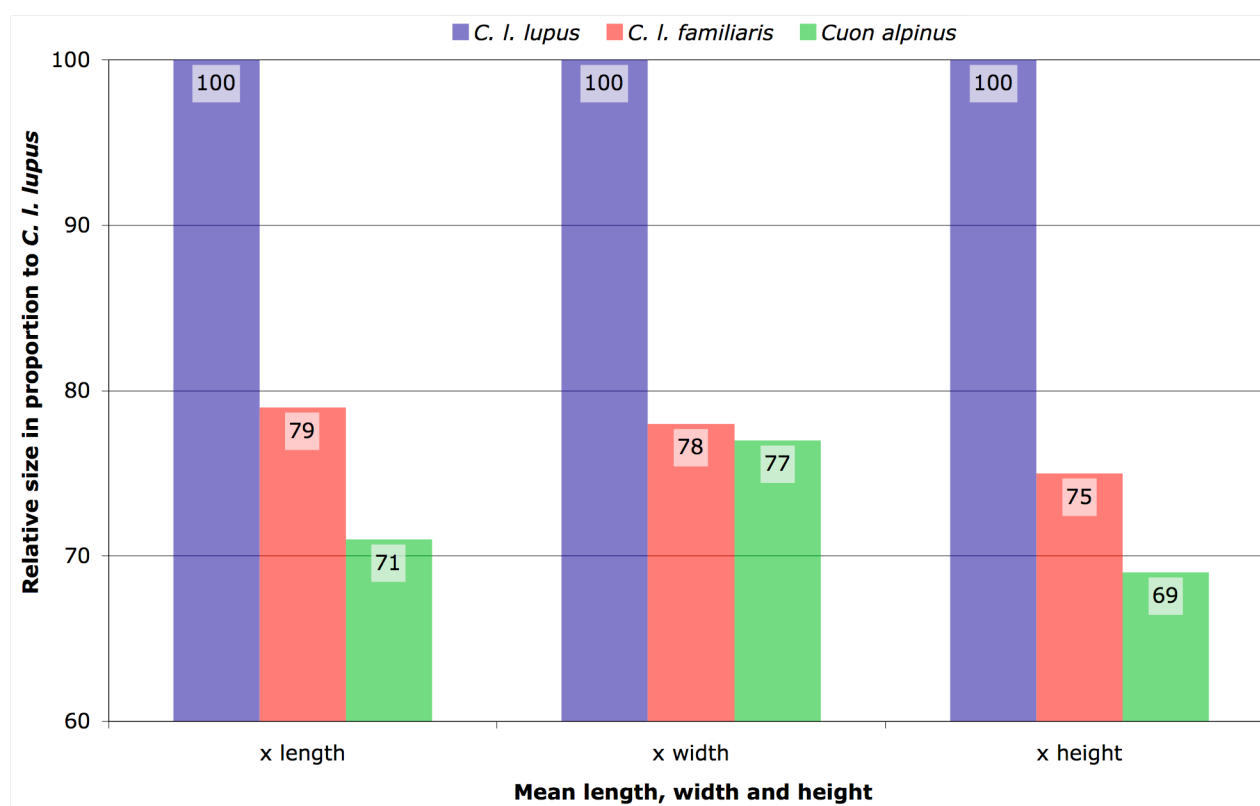
For the average *C. l. familiaris* specimen mandible lengths, widths and heights are reduced in proportion to *C. l. lupus* in similar amounts: at first sight there is no very clear trend in reduction (table 4.22 and fig. 4.19). A closer look reveals that there is slightly more reduction in width and height than in length, which confirms the initial qualitative (visual) comparison of *C. l. familiaris* with *C. l. lupus* (before any parameters were taken), which had already shown that compared to *C. l. lupus* *C. l. familiaris* is smaller and more fragile (and *Cuon alpinus* smaller and sturdier).

For the average *Cuon alpinus* specimen the reduction of mandible lengths, widths and heights in proportion to *C. l. lupus* is less similar (table 4.22 and fig. 4.19). Although the differences in reduction are not very large, a clear trend can be seen: the mandible length and height of *Cuon alpinus* are reduced with approximately 30% compared to *C. l. lupus*, while the width is only reduced with 23%. This indicates that *Cuon alpinus* mandibles have slightly other proportions than *Canis* mandibles: *Cuon alpinus* mandibles are sturdier, because they are relatively wider (as observed in 4.1.1.2). *Cuon alpinus* shows on average more reduction in size compared to *C. l. lupus* than *C. l. familiaris*.

Compared to the results of the *Cuon alpinus* specimen from Pérez Ripoll et al. (2010), *Cuons* in this dataset show more reduction in all three parameters (table 4.22). Moreover, another trend is observed: Pérez Ripoll et al. (2010) found that the width was less reduced than length and that height was even less reduced than width. In this dataset the *Cuon alpinus* mandible length and height are reduced with similar amounts and only the width is less reduced than these two parameters. Although another trend is observed, the final result is the same: *Cuon alpinus* mandibles are sturdier than *Canis* mandibles.

**Table 4.22: Size of the mandible length, width and height of the comparative material given as average size (x) and relative size in proportion to *C. I. lupus* (%).** Given are the mean values of the mandible length ( $P_1-M_2$ ), width ( $i-i'$ ) and height ( $h-h'$   $P_3$ ) of the three comparative (sub)species and the relative size in these three subparameters in proportion to the average comparative *C. I. lupus* reference value (x *C. I. lupus* for each subparameter). In brackets ( ) the amount of reduction in proportion to *C. I. lupus* is given. Also included is the amount of reduction in *Cuon alpinus* mandibles for these three subparameters according to Pérez Ripoll et al. (2010).

Canidae material		Size of mandible L, W and H		
		length	width	height
<i>C. I. lupus</i>	x	85,92	14,57	26,52
	%	100	100	100
<i>C. I. familiaris</i>	x	68,01	11,4	19,76
	%	79 (21)	78 (22)	74 (25)
<i>Cuon alpinus</i>	x	61,37	11,2	18,35
	%	71 (29)	76 (23)	69 (31)
Pérez Ripoll et al. (2010)	%	18	10	4



**Figure 4.19: Bar chart of the average mandible length, width and height of the comparative material in proportion to *C. I. lupus* (%).** For each comparative (sub)species is indicated how much the mandible length, width and height are reduced with respect to the average comparative *C. I. lupus* reference value (x *C. I. lupus* for each subparameter, table 4.22).

#### 4.2.5.2 Results fossil North Sea material

For all values of the fossils mentioned below hereby is referred to table 4.23 below. For comparison of the values of the fossil North Sea specimens to ratios of the comparative material: see table 4.22 and fig. 4.19. Not all 13 fossil North Sea specimens had values for all three parameters, thus for only 10 specimens ratios could be calculated.

**Specimen 534** misses a large anterior part of its hemimandible and has thus no values for mandible length, width and height (appendix I). Ratios could not be calculated.

**Specimens 535 and NMR90** only have values for mandible width, which both are 85% of the width of the average comparative *C. I. lupus* reference value (table 4.23).



**Specimen 667** shows reduction in length, width and height of respectively 23, 15 and 28% (table 4.23). In this specimen width is thus much less reduced in size compared to the average comparative *C. l. lupus* reference value than length and height (as *Cuon alpinus*), but the height is more reduced than the length (as *C. l. familiaris*). The effect of the width is slightly higher than the effect of height, thus the mandible is slightly sturdier than the average *C. l. lupus* specimen.

**Specimen 1683** shows an increase in length, width and height of respectively 12, 16 and 11%. This specimen is thus longer, wider and has greater heights below its  $P_3$  than the average *C. l. lupus* specimen, while *C. l. familiaris* and *Cuon alpinus* show reduction on these points.

**Specimen 2103** shows reduction in length, width and height of respectively 15, 24 and 13%. In this specimen the length and width of the mandible are thus reduced with similar amounts, while the width is reduced more; a trend that is opposite to the trend observed in an average *Cuon alpinus* specimen. This hemimandible is more fragile than the average *C. l. lupus* specimen.

**Specimen 2104** shows reduction in length, width and height of respectively 17, 20 and 16%. In this specimen the length, width and height of the mandible are reduced with similar amounts (although width is slightly more reduced than length and height), which is most similar to the *C. l. familiaris* trend. This hemimandible is mostly smaller (and slightly more fragile) than the average *C. l. lupus* specimen.

**Specimen 2196** shows an increase in length, width and height of respectively 10, 9 and 13%. This specimen is thus longer, wider and has greater heights below its  $P_3$  than the average *C. l. lupus* specimen, while *C. l. familiaris* and *Cuon alpinus* show reduction on these points.

**Specimen 2329** shows reduction in length, width and height of respectively -3, 10 and 0%. This specimen is thus very comparable in size to the average *C. l. lupus* specimen, but is more fragile, because it shows a reduction in width and not in length and height (which is in accordance with the *C. l. familiaris* trend).

**Specimen 2620** shows an increase in length, width and height of respectively 14, 2 and 13%. This specimen is thus longer, wider and has greater heights below its  $P_3$  than the average *C. l. lupus* specimen, while *C. l. familiaris* and *Cuon alpinus* show reduction on these points. Since width shows less increase than length and height, this specimen is more fragile than the average *C. l. lupus* specimen.

**Specimen 3219** shows reduction in length, width and height of respectively 15, 14 and 16%. In this specimen the length, width and height of the mandible are reduced with similar amounts, unlike the trend observed in *Cuon alpinus*.

**Specimen 3293** shows an increase in length, width and height of respectively 4, 6 and -4%. This specimen is thus very comparable in size to the average *C. l. lupus* specimen.

**Specimen NMR89** shows reduction in length, width and height of respectively -5, 12 and 25% (table 4.23). This specimen is thus comparable in length to the average *C. l. lupus* specimen, but is smaller and has much lower heights below its  $P_3$ . This specimen shows a trend opposite to that observed in *Cuon alpinus* by Pérez Ripoll et al. (2010) and is more fragile than the average *C. l. lupus* specimen.

**Table 4.23: Mandible length ( $P_1$ - $M_2$ ), width ( $i$ - $i'$ ) and height ( $h$ - $h'$   $P_3$ ) of the fossil North Sea specimens in proportion to the average comparative *C. l. lupus* value (in %). Ratios were calculated dividing the absolute measured value of the fossil North Sea specimen for each subparameter (appendix XIII) over the average value of the *C. l. lupus* comparative dataset for that parameter (table 4.22), multiplying by 100 to obtain percentages.**

Fossils	Relative size of mandible L, W and H in proportion to <i>C. l. lupus</i> (%)		
	length	width	height
535	-	85	-
667	77	85	72
1683	112	116	111
2103	85	76	87
2104	83	80	84
2196	110	109	113
2329	103	90	100
2620	114	102	113
3219	85	86	84
3293	104	106	96
NMR89	105	88	75
NMR90	-	85	-

## 4.3 Ramus

### 4.3.1 Distance *a-d* and *e-e'*

Distances *a-d* and *e-e'* are indicators for the size of the mandible (since the size of the ramus will be in proportion to the other dimensions of the mandible) and can thus possibly be used to identify the Fossil North Sea specimens (fig. IV.1).

#### 4.3.1.1 Results comparative material

For all values mentioned below see both table 4.24 and fig. 4.20 unless stated otherwise.

**x** For both distances *C. l. lupus* has on average the largest value, while both *C. l. familiaris* and *Cuon alpinus* have significantly smaller values and lie very close together (table 4.24 and fig. 4.20).

**SD vs. n** For parameter *a-d* the variation in both *Canis* species is very similar, but the standard deviation of *C. l. lupus* is slightly bigger than that of *C. l. familiaris*, although its sample size is less than twice the size of that of *C. l. familiaris* (table 4.24). For parameter *e-e'* the standard deviation of *C. l. familiaris* is larger than that of *C. l. lupus*, while also its sample size is larger. For both parameters the *Cuon alpinus* sample size lies in between those of the *Canis* species, while the variation of this species is the lowest of all comparative species.

**Sample ranges** Values in table 4.24 indicate that the *Cuon alpinus* and *C. l. lupus* ranges overlap significantly with each other, but fig. 4.20 shows that this is caused by one *C. l. lupus* specimen (*lupus-m*) that is the only *C. l. lupus* that plots within the *Cuon alpinus* data cloud. Apart from this specimen the *Cuon alpinus* and *C. l. lupus* data clouds are nicely separated, with the *Cuon alpinus* data cloud plotting in the lower ranges of the figure and *C. l. lupus* in the upper part. *C. l. familiaris*, as always, overlaps significantly with these both species plotting from lower than the *Cuon alpinus* minimum to close to the *C. l. lupus* mean. Also for these parameters one can make a slight distinction within the *C. l. familiaris* group, separating the fossil specimens from the Netherlands from the recent specimens from Suriname. As for previous parameters, the recent specimens from Suriname plot over the entire *C. l. familiaris* range and form the upper- and lowermost values, while the fossil specimens from the Netherlands are slightly more concentrated in the middle of the graph and do not have values for *a-d* and *e-e'* as small as the recent specimens from Suriname (fig. VII.8). Data points (specimens) of all three comparative species are quite evenly distributed along their ranges and there are no remarkable specimens that deviate much from this linear band of data points (apart from *lupus-m* that plotted quite low compared to the other *C. l. lupus* specimens) (fig. 4.20).

**Population ranges** For the population ranges there is still overlap between the *Cuon alpinus* and *C. l. lupus* ranges. *C. l. familiaris* overlaps significantly with these both species, plotting from lower than the *Cuon alpinus* minimum to just below the *C. l. lupus* mean (fig. 4.20).

**Trend lines** Parameters *a-d* and *e-e'* are quite similar and as a result the data clouds of the three comparative species plot quite linearly in fig. 4.20. All three comparative species have similar values for *a-d* in proportion to *e-e'*; there are no significant differences. Trend lines are thus not helpful in the determination of the identity of the fossil North Sea specimens and will not be plotted or discussed.

**Table 4.24: Statistics of the parameters 'Distance' *a-d* (left) and *e-e'* (right) of the comparative material (in mm).**  
Legend: see table 4.1.

Statistics	Distance <i>a-d</i>			Distance <i>e-e'</i>		
	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>
Sample size (n)	14	39	27	14	39	27
Sample mean (x)	53,37	40,77	40,67	71,66	55,68	55,21
Standard deviation (SD)	5,86	5,67	2,72	6,78	7,37	3,59
Minimum (MIN)	41,52	30,44	32,77	58,32	41,38	46,66
Maximum (MAX)	63,98	51,62	48,14	86,21	71,25	65,47
Sample range MIN	40,32	29,24	31,57	56,49	39,55	44,83
Sample range MAX	65,18	52,82	49,34	88,04	73,08	67,30
Population range MIN	41,65	29,43	35,23	58,09	40,94	48,04
Population range MAX	65,09	52,11	46,10	85,22	70,42	62,38

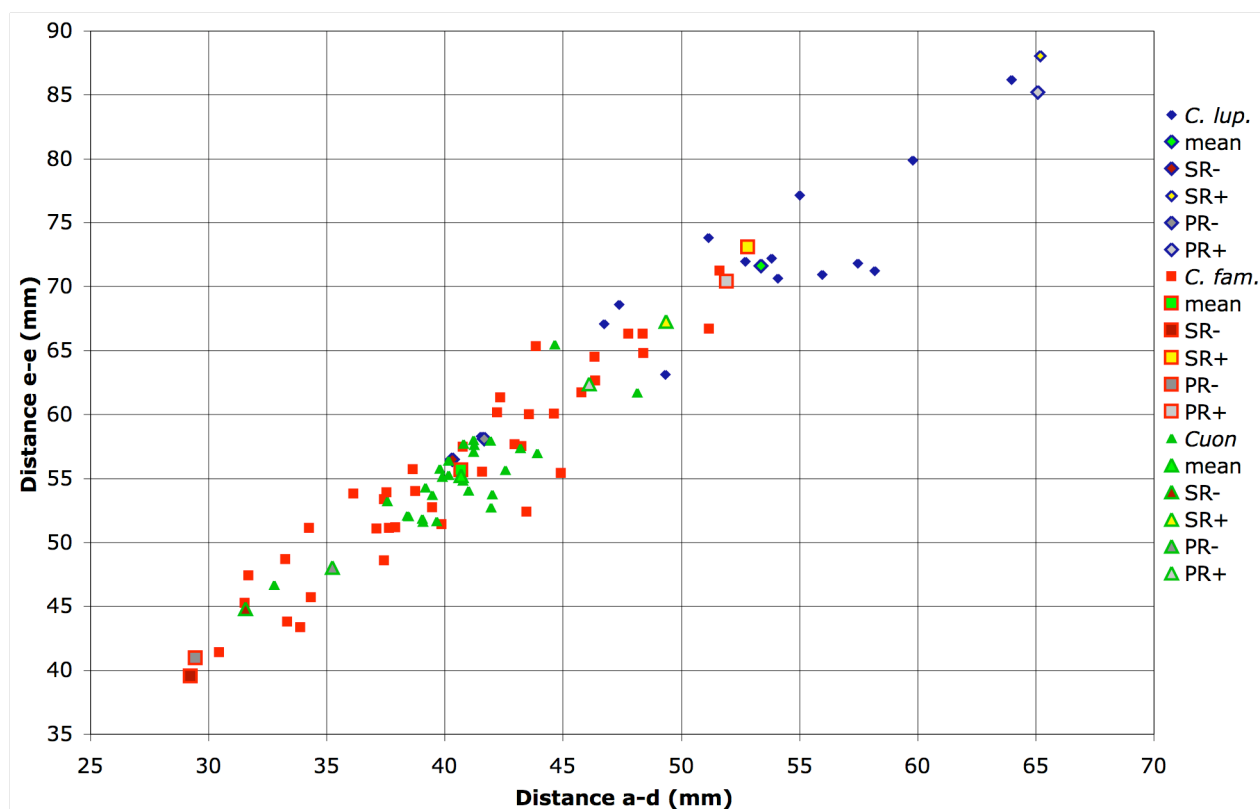


Figure 4.20: Scatter plot of parameters 'Distance' *a-d* vs. *e-e'* for the comparative material (in mm). Legend, see table 4.1.

#### 4.3.1.2 Results fossil North Sea material

In not all 13 fossil North Sea specimens the ramus was intact, thus for only 7 specimens values for *a-d* and *e-e'* could be obtained and only these specimens could be plotted in fig. 4.21 below. For 3 of these 7 fossil North Sea specimens, parameters *a-d* and *e-e'* could not be measured directly on the specimen to obtain the exact value of that specific specimen, because these specimens are not complete anymore (parts of the ramus are eroded, appendix I). But for all of these specimens a sufficiently large part of the ramus remained to make a reasonable estimate of the two parameters (as described in 2.2.2). Thus keep in mind that for some of the following fossil North Sea specimens the specimen ranges are estimates based on specimens of the comparative material.

##### Specimen 534

Specimen 534 is a posterior part of a hemimandible, but the ramus is partly eroded and points *a*, *d* and *e* (appendix I and fig. IV.1) are missing, thus parameters *a-d* and *e-e'* could not be measured directly on this specimen. From other results (teeth int. al.) was already known that specimen 534 very probably is not *Cuon alpinus*. Moreover specimen 534 is a quite large mandible part: it is bigger in size than all comparative *C. l. familiaris* and *Cuon alpinus* specimens. Therefore 534 was compared to comparative *C. l. lupus* specimens and it compared best in size and shape to the ramus of *C. l. lupus* specimen *lupus-d*. This specimen was used to estimate the two distances *a-d* and *e-e'* for this fossil North Sea specimen (note that this *C. l. lupus* specimen is another specimen than the specimens that were used to estimate the mandible length, 4.1.1.2). Specimen 534 falls entirely within the sample and population ranges of *C. l. lupus* and entirely outside (above) the sample and population ranges of *Cuon alpinus* for both parameters (table 4.25 and fig. 4.21). This specimen range also falls entirely outside (above) the *C. l. familiaris* sample and population range for parameter *a-d*. For parameter *e-e'* 534 falls entirely within the sample range of *C. l. familiaris* and partly within corresponding population range. The mean value of 534 for parameter *a-d* (58.18 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 4.81 mm between the two mean values) and much less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with respectively 17.41 and 17.51 mm) (mean values can be found in appendix XIII). Values are comparable for *e-e'*.

##### Specimens 535, 2620, 3219, 3293 and NMR89

The ramus of these five fossil North Sea specimens is either absent or considerably eroded (appendix I), thus parameters *a-d* and *e-e'* could not be taken for these specimens.

### Specimen 667

The ramus of this specimen is quite intact, thus the values for parameters *a-d* and *e-e'* were taken on the specimen itself and are no estimates. The specimen range of this specimen falls in all sample and population ranges of all three comparative species (fossil part of the *C. l. familiaris* sample range, fig. VII.8), although only partly in the *Cuon alpinus* population ranges for both parameters (table 4.25 and fig. 4.21). The mean value of 667 for parameter *a-d* (46.17 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 5.40 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 5.50 mm) and most dissimilar to the average *C. l. lupus* specimen (with 7.20 mm) (appendix XIII). The values and trend are similar for *e-e'*.

### Specimen 2103

The values for specimen 2103 were also taken on the specimen itself. Specimen 2103 falls entirely within the sample and population ranges of *C. l. familiaris* (fossil part) and *Cuon alpinus* for both parameters (table 4.25 and fig. 4.21). It also falls entirely within the *C. l. lupus* sample and population ranges for *a-d*, but falls partly outside (below) the *C. l. lupus* sample and population range for *e-e'*. The mean value of 2103 for parameter *a-d* (43.89 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 3.12 mm between the two mean values), slightly less similar to the average *Cuon alpinus* specimen (with 3.22 mm) and most dissimilar to the average *C. l. lupus* specimen (with 9.48 mm) (appendix XIII). This trend is similar for *e-e'*, although values are a little more extreme for this parameter (2103 is even more similar to *C. l. familiaris* and more dissimilar to *C. l. lupus*).

### Specimen 2104

Results of specimen 2104 are quite similar to those of the previous specimen. Specimen 2104 falls entirely within the sample and population ranges of *C. l. familiaris* (fossil part, fig. VII.8) and *Cuon alpinus*, but partly outside (below) the *C. l. lupus* sample and population ranges for both parameters (table 4.25 and fig. 4.21). The mean value of 2104 for parameter *a-d* (41.51 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.74 mm between the two mean values), slightly less similar to the average *Cuon alpinus* specimen (with 0.84 mm) and most dissimilar to the average *C. l. lupus* specimen (with 11.86 mm). The trend and values are similar for *e-e'* (appendix XIII).

### Specimen 2196

Specimen 2196 is one of three largest fossil North Sea specimens and is bigger than all comparative *C. l. familiaris* and *Cuon alpinus* material. Results of other parameters (teeth int. al.) indicated that this specimen is very probably a *Canis* specimen and not *Cuon alpinus*. Qua appearance 2196 looks far too large and robust to be a *Cuon alpinus* or *C. l. familiaris* specimen and it compares very well to comparative *C. l. lupus* specimen *lupus-c*, the same specimen that was used to estimate this specimens' values of the mandible length (4.1.1.2). Although most part of the ramus of 2196 is eroded, the lower part is still intact and it could be established that this ramus was very similar in shape and size to the ramus of *lupus-c*, thus this comparative specimen was used to estimate the two distances *a-d* and *e-e'* for this fossil North Sea specimen. Specimen 2196 falls entirely outside (above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus*, but inside the sample ranges of *C. l. lupus* (for both parameters) (table 4.25 and fig. 4.21). This specimen is even quite large for a *C. l. lupus* specimen: it falls partly outside (above) the *C. l. lupus* population ranges. As expected from these results, the mean value of this specimen for parameter *a-d* (63.98 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 10.61 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with respectively 23.21 and 23.31 mm) (appendix XIII). The trend and values are similar for *e-e'*.

### Specimen 2329

Specimen 2329 falls entirely within the sample and population ranges of *C. l. lupus* and entirely outside (above) the sample and population ranges of *Cuon alpinus* for both parameters (table 4.25 and fig. 4.21). It also falls outside (above) the sample and population ranges of *C. l. familiaris* for *a-d* and outside (above) the *C. l. familiaris* population range of *e-e'*. Specimen 2329 only partly falls outside (above) the *C. l. familiaris* sample range for *e-e'*. The mean value of this specimen for parameter *a-d* (55.44 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 2.07 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with respectively 14.67 and 14.77 mm) (appendix XIII). The trend and values are similar for *e-e'*.

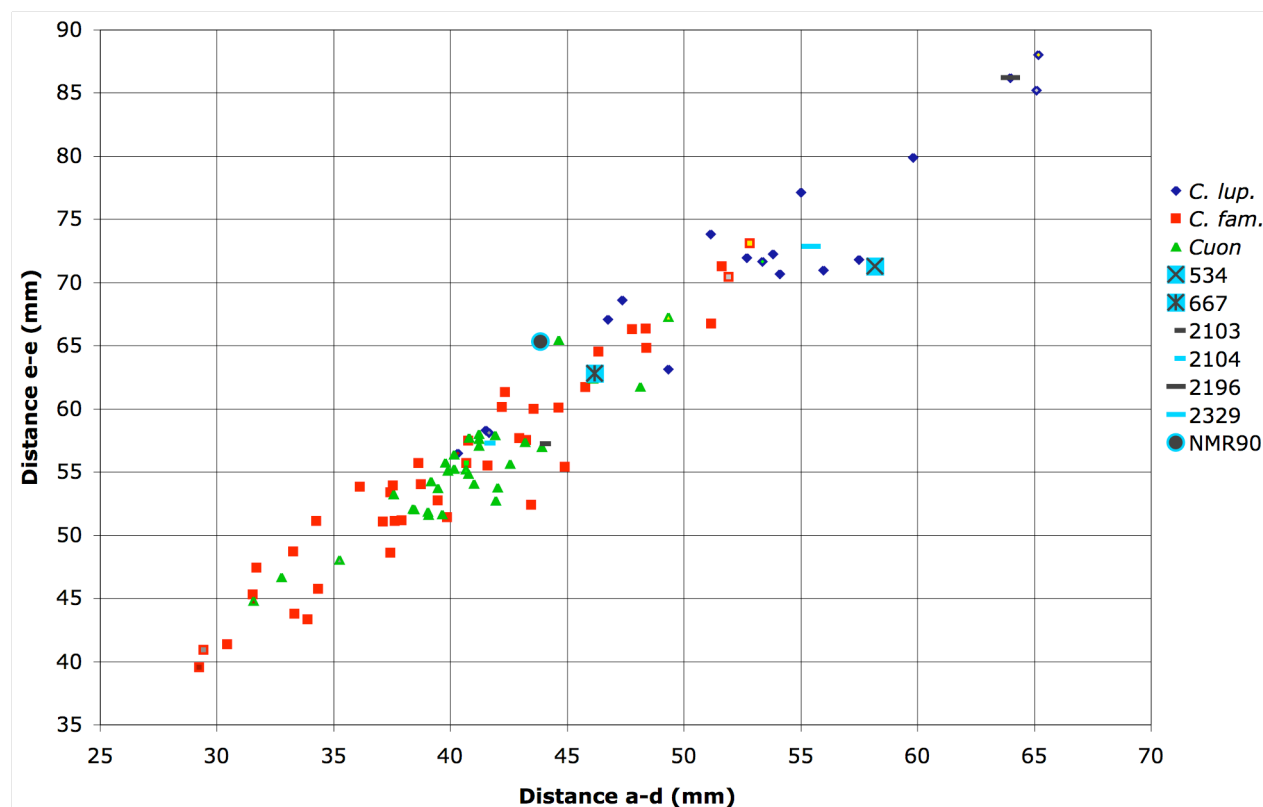
### Specimen NMR90

Specimen NMR90 is a posterior part of a hemimandible, but the ramus is partly eroded and points *a*, *d* and *e* are missing (appendix I and fig. IV.1). Parameters *a-d* and *e-e'* could thus not be measured directly on NMR90. As was explained extensively in 4.1.1.2 NMR90 compares best in size and shape to *C. l. familiaris* specimens, therefore NMR90 was compared to comparative *C. l. familiaris* specimens to obtain values for *a-d* and *e-e'*. It compared best in size and shape to the ramus of *C. l. familiaris* specimen 34601. This

specimen was used to estimate the two distances  $a-d$  and  $e-e'$  for this fossil North Sea specimen. (Note that this *C. l. familiaris* specimen is one of the specimens that were used to estimate the mandible length, 4.1.1.2). NMR90 falls entirely within the sample and population ranges of both *Canis* species (for both parameters) (fossil part of the *C. l. familiaris* sample range, fig. VII.8). It also falls entirely within the sample and population ranges of *Cuon alpinus* for  $a-d$  and within the *Cuon alpinus* sample range of parameter  $e-e'$ , but entirely outside (above) the corresponding *Cuon alpinus* population range (table 4.25 and fig. 4.21). The mean value of NMR90 for parameter  $a-d$  (43.86 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 3.09 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 3.19 mm) and most dissimilar to the average *C. l. lupus* specimen (with 9.51 mm) (appendix XIII). For  $e-e'$  NMR90 is most similar to the average *C. l. lupus* specimen (with 6.35 mm) and less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with respectively 9.63 and 10.10 mm).

**Table 4.25: Comparison of the specimen ranges of the fossil North Sea specimens with the sample and population ranges of the comparative material for parameters 'Distance'  $a-d$  (left) and  $e-e'$  (right) (in mm).** Sample and population ranges of the comparative material are as given in table 4.24. Specimen ranges were calculated as explained in table 4.2.

Canidae material		Distance $a-d$				Distance $e-e'$			
		- Sample range +		- Population range +		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	40,32	65,18	41,65	65,09	56,49	88,04	58,09	85,22
	<i>C. l. familiaris</i>	29,24	52,82	29,43	52,11	39,55	73,08	40,94	70,42
	<i>Cuon alpinus</i>	31,57	49,34	35,23	46,10	44,83	67,30	48,04	62,38
Fossil North Sea	534	56,98	59,38	-	-	69,42	73,08	-	-
	667	44,97	47,37	-	-	60,99	64,65	-	-
	2103	42,69	45,09	-	-	55,42	59,08	-	-
	2104	40,31	42,71	-	-	55,45	59,11	-	-
	2196	62,78	65,18	-	-	84,38	88,04	-	-
	2329	54,24	56,64	-	-	71,00	74,66	-	-
	NMR90	42,66	45,06	-	-	63,48	67,14	-	-



**Figure 4.21: Scatter plot of parameters 'Distance'  $a-d$  vs.  $e-e'$  for the fossil North Sea specimens and the comparative material (in mm).** Legend, see tables 4.1 and 4.2.

### 4.3.2 Coronoid angle

According to Pérez Ripoll et al. (2010) a general morphological character of the mandibles of *Cuon alpinus* as compared to present-day *C. l. lupus* would be that the angle between the coronoid process and the body of the mandible is smaller in *Cuon alpinus* than in *C. l. lupus*. It was thus assumed that the coronoid angle would be another parameter that could be used to distinguish between *Cuon alpinus* and *C. l. lupus* and to identify the fossil North Sea specimens (fig. IV.1). But a brief analysis of the results revealed otherwise.

*Cuon alpinus* has on average indeed a slightly smaller coronoid angle (106°) than *C. l. lupus* (108°, see appendix XIII for the statistics of this parameter), but results presented table 4.26 show that the sample and population ranges of *Cuon alpinus*, *C. l. familiaris* and *C. l. lupus* are very similar. Although the largest angles are indeed observed in *C. l. lupus*, the smallest angles are observed in *C. l. familiaris* and not in *Cuon alpinus*. The minima of the *Cuon alpinus* ranges are even one degree larger than the *C. l. lupus* minima. Overall there are no significant differences between the three comparative species (as was the case for previous parameters): there are hardly angles that are specific for one single species. A short comparison of the specimen ranges of the fossil North Sea specimens with these sample and population ranges revealed, that most specimens fall within both ranges of all three comparative species (table X.2). Only four specimens just partially overlap with one or both ranges. Since these results are not conclusive about the identity of the fossil specimens (they indicate that the fossil North Sea specimens could still be either *Canis* or *Cuon alpinus*), these results will not be analyzed or discussed any further.

**Table 4.26: Sample and population ranges of the comparative material for parameter ‘Coronoid angle’ (in °).** For more detailed results (statistics of the comparative material and individual values of the fossil North Sea specimens): see appendix XIII and table X.2.

Canidae material		Coronoid angle (°)			
		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	98	118	101	115
	<i>C. l. familiaris</i>	91	114	94	111
	<i>Cuon alpinus</i>	99	114	102	111

### 4.3.3 Aboral border of the ramus

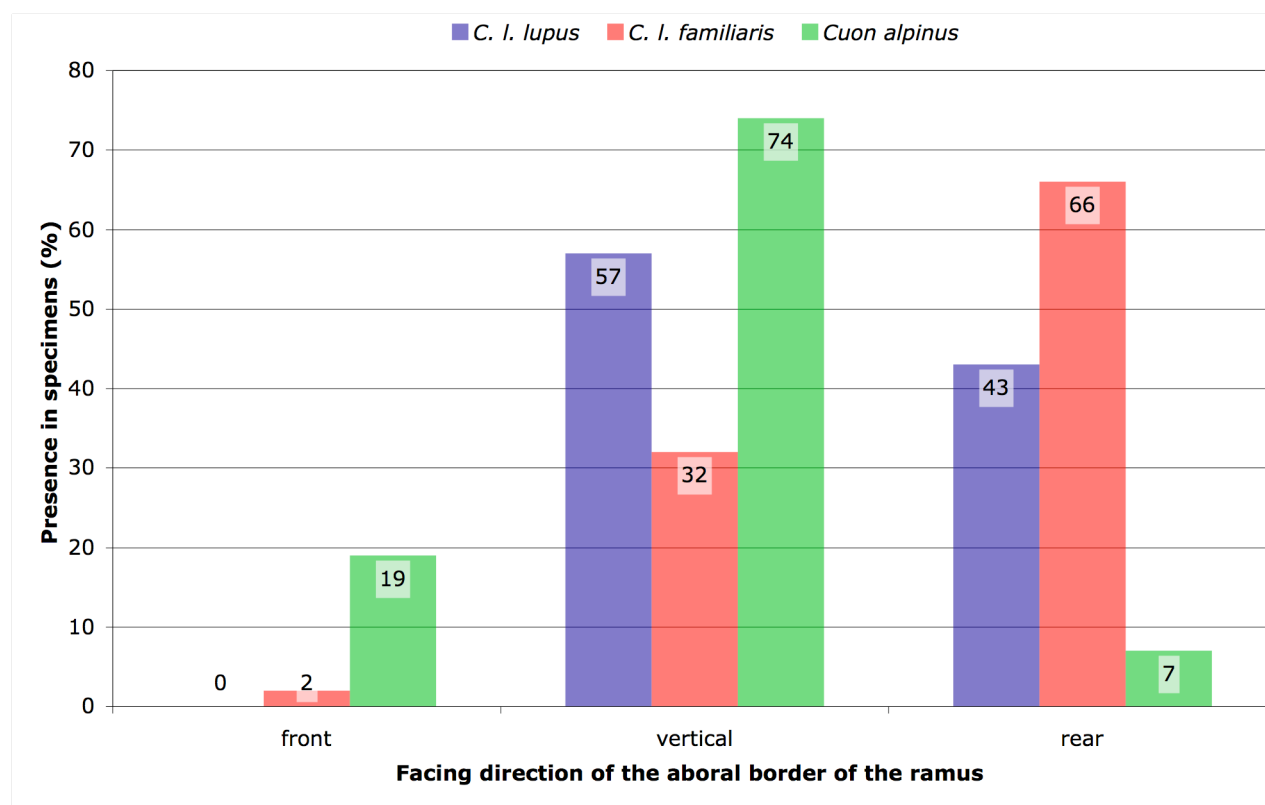
According to Pérez Ripoll et al. (2010) another general morphological character of the mandibles of *Cuon alpinus* as compared to present-day *C. l. lupus* would be that the aboral border of the ramus typically would face towards the anterior part of the mandible in *Cuon alpinus* and face towards the posterior part of the mandible in *C. l. lupus* (fig. IV.3). But the results of this study indicate that this difference between *Cuon alpinus* and *C. l. lupus* is not as solid as is presented by Pérez Ripoll et al. (2010).

#### 4.3.3.1 Results comparative material

Table 4.27 and fig. 4.22 show a summary of the results of the comparative material (for all individual values of the comparative specimens see appendix XIII). In this dataset the aboral border hardly respectively never faces the front in *C. l. familiaris* and *C. l. lupus*, while this is more common in *Cuon alpinus* (19%) (table 4.27). On the other hand, the aboral border hardly faces the rear in *Cuon alpinus* (7%), while this is much more common the both *Canis* species (43% for *C. l. lupus* and 66% for *C. l. familiaris*). So far results coincide with those of Pérez Ripoll et al. (2010), in that facing front is more typical in *Cuon alpinus* and facing rear more in *Canis* (fig. 4.22). But there is also a significant amount of specimens that shows no clear facing direction of the aboral border, as can clearly be seen in fig. 4.22. In *C. l. lupus* and *Cuon alpinus* most specimens have a vertical aboral border of the ramus: it does not face clearly towards the front or rear. Although in *C. l. familiaris* most specimens have a rear facing aboral border, a significant amount of the specimens also shows no clear facing direction. For this parameter there are no significant differences between the fossil *C. l. familiaris* specimens from the Netherlands and the recent specimens from Suriname: the two groups have a similar amount of specimens with rear and vertical facing borders (appendix XIII). The specimen with the front facing border is a recent specimen from Suriname.

**Table 4.27: Statistics of the parameter 'Aboral border of the ramus' of the comparative material (absolute counted specimens (#) and %).** The aboral border of the ramus can face towards the anterior part of the mandible (front), towards the posterior part of the mandible (rear) or not face in a specific direction at all (vertical). Sample sizes of the three comparative (sub)species were: *C. l. lupus* (14), *C. l. familiaris* (41), *Cuon alpinus* (27).

Canidae material		Facing direction of the aboral border of the ramus		
		front	vertical	rear
<i>C. l. lupus</i>	#	-	8	6
	%	-	57	43
<i>C. l. familiaris</i>	#	1	13	27
	%	2	32	66
<i>Cuon alpinus</i>	#	5	20	2
	%	19	74	7



**Figure 4.22: Bar chart of the parameter 'Aboral border of the ramus' for the comparative material (in %).** For each option is indicated how much percent of the specimens of the total sample sizes of the three comparative (sub)species were encountered with that option. For absolute counted specimens, sample sizes and the legend, see table 4.27.

#### 4.3.3.2 Results fossil North Sea material

Specimens 535, 1683, 2196, 2620, 3219, 3293, NMR89 and NMR90 miss a large part of or the entire ramus, thus do not have data for this parameter (appendix I and XIII). In NMR90 the lowermost part of the aboral border is still intact and seems to face slightly towards the front (which is actually hard to conclude, since a large anterior part of the mandible is eroded as a result of which a reference line is missing). This initial front facing of the aboral border can also be seen in specimens that have a clearly rear facing aboral border (for example comparative *C. l. familiaris* specimens 34601 and 18051 and fossil North Sea specimen 2103, appendix I). This is the result of the curvature that is often seen in the aboral border. It can thus not be concluded whether the aboral border faced the front or the rear in specimen NMR90.

Specimens 534, 667, 2103, 2104 and 2329 have an aboral border of the ramus that faces the rear (appendix I and XIII).

### 4.3.4 Anterior border of the coronoid process

A third general morphological character of the mandibles of *Cuon alpinus* as compared to present-day *C. l. lupus* is that the anterior border of the coronoid process is well developed and rounded in *Cuon alpinus*, but thin in *C. l. lupus* (Pérez Ripoll et al., 2010, fig. IV.3). If results of this study indicate the same, this parameter can be used to identify the fossil North Sea specimens. Note that this parameter is relative: the thickness of the anterior border is termed thin or thick compared to the rest of the hemimandible.

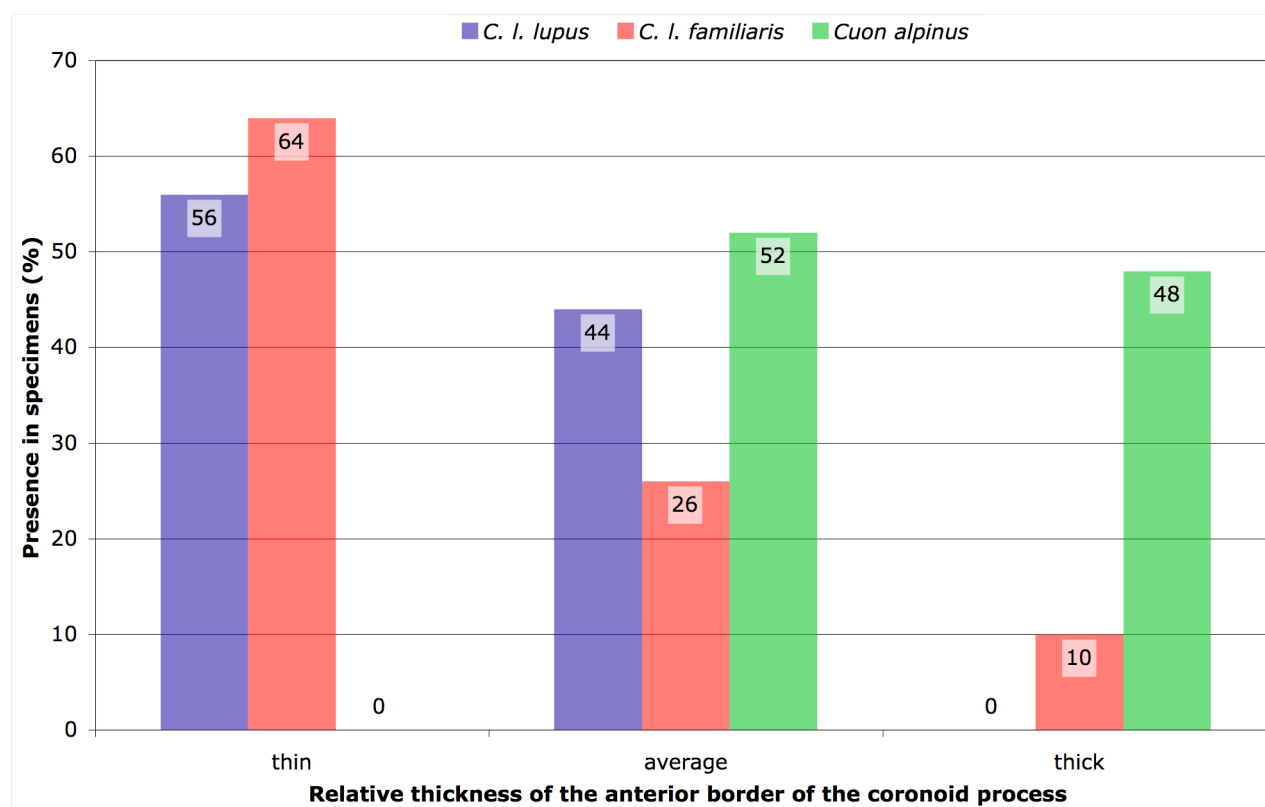
#### 4.3.4.1 Results comparative material

It was observed that in *Canis* specimens the anterior border is small and clearly sticks out compared to the rest of the hemimandible: it is a distinct ridge, while in *Cuon alpinus* the border is broader, more rounded and less distinct (fig. IV.3). Table 4.28 and fig. 4.23 show a summary the results of the comparative material (for all individual values of the comparative specimens, see appendix XIII). In this dataset more than 50% of both *Canis* species have clearly thin and distinct anterior borders of the coronoid process, while this border is never extremely thin in *Cuon alpinus*. In almost 50% of the *Cuon alpinus* specimens the anterior border is round and well developed, while the occurrence of a thick anterior border hardly occurs in *C. l. familiaris* and never in *C. l. lupus*. So far results coincide with those of Pérez Ripoll et al. (2010), in that a well developed border is more typical in *Cuon alpinus* and a thin border more in *Canis*. There is also a significant amount of specimens that shows no typical appearance of the anterior border, something Pérez Ripoll et al. (2010) did not mention. Approximately half of the *C. l. lupus* and *Cuon alpinus* specimens and a significant amount of the *C. l. familiaris* specimens (26%) do not have a clearly thin or thick anterior border. For this parameter there are no significant differences between the fossil *C. l. familiaris* specimens from the Netherlands and the recent specimens from Suriname: the two groups have a similar amount of specimens with thick, thin and average anterior borders (appendix XIII).

**Table 4.28: Statistics of the parameter ‘Anterior border of the coronoid process’ of the comparative material (absolute counted specimens (#) and %).** The anterior border of the coronoid process can be thin, well developed and round (thick) or neither of these two options (average). Sample sizes of the comparative (sub)species were: *C. l. lupus* (18), *C. l. familiaris* (42), *Cuon alpinus* (27).

Canidae material		Relative thickness of the anterior border of the coronoid process		
		thin	average	thick
<i>C. l. lupus</i>	#	10	8	-
	%	56	44	-
<i>C. l. familiaris</i>	#	27	11	4
	%	64	26	10
<i>Cuon alpinus</i>	#	-	14	13
	%	-	52	48





**Figure 4.23:** Bar chart of the parameter 'Anterior border of the coronoid process' for the comparative material (in %). For each option is indicated how much percent of the specimens of the total sample sizes of the three comparative (sub)species were encountered with that option. For absolute counted specimens, sample sizes and the legend, see table 4.28.

#### 4.3.4.2 Results fossil North Sea material

See appendix I for photos of the 13 fossil North Sea specimens and the appearance of their anterior borders compared to the typical *C. l. lupus* and *Cuon alpinus* appearances (fig. IV.3). See appendix XIII for results of the specimens.

##### Specimens 534 and 2329

These two specimens are very similar in size and shape and can very well be compared. Specimen 534 does not show a distinct ridge that clearly sticks out compared to the rest of the mandible (appendix I). This ridge is quite broad and does not resemble the typical *Canis* appearance of the anterior border, but neither looks like the broad border as observed in *Cuon alpinus* (fig. IV.3). This specimen is classified as having a thick anterior border (although not typically *Cuon alpinus*) (appendix XIII). The anterior border of specimen 2329 on the other hand clearly sticks out from the rest of the mandible. The border is not extremely thin compared to the rest of the mandible as in a textbook example of the anterior border of a *Canis* specimen, but is certainly not rounded and does not have a *Cuon alpinus* appearance. Specimen 2329 has a thin border (appendix I and XIII).

##### Specimens 535, 2196, 3219 and NMR89

In specimens 535, 2196 and 3219 a large part of the ramus is missing, thus the appearance of the anterior border could not be established (appendix I). In NMR89 a large part of the ramus is still present, but the edges are considerably eroded and, as a result, rounded. It is impossible to establish what the appearance of anterior border of the ramus was before erosion.

##### Specimens 667, 2103 and 2104

Specimens 667 and 2103 have typical *Canis* borders: the anterior border of these specimens is very thin and distinct compared to the rest of the hemimandible (appendix I). Although specimens 2103 and 2104 looked very similar to each other in previous parameters, the anterior border of the ramus of specimen 2104 looks slightly different than the border of 2103. In absolute size this anterior border is similar to the border of specimen 2329, but the size of the entire mandible is much smaller. The anterior border of specimen 2104 is thus not very thin, as the typical *Canis* appearance, but neither has a rounded appearance. The anterior border of specimen 2104 is classified as average (appendix XIII).

### Specimens 1683, 2620, 3293 and NMR90

In specimens 2620 and 3293 the entire ramus is eroded, but a small part of the anterior border, which is large enough to determine its appearance, is still present on the mandible (appendix I). The anterior borders of these two specimens are both very small, clearly stick out compared to the rest of the mandible and are classified as thin (appendix XIII). The border of specimen 1683 is in absolute size slightly thicker than the anterior borders of specimens 2620 and 3293, but this specimen is one of the largest fossil North Sea specimens and was also more heavily built than the comparative *C. l. lupus* material (4.1.1.2). Moreover the anterior border clearly sticks out from the rest of the mandible. This specimen is thus also classified as having a thin border. In NMR90 a large part of the ramus is still present and it can clearly be seen that the anterior border is thin and distinct and not broad and rounded as in *Cuon alpinus* (appendix I).

## 4.3.5 Angular process

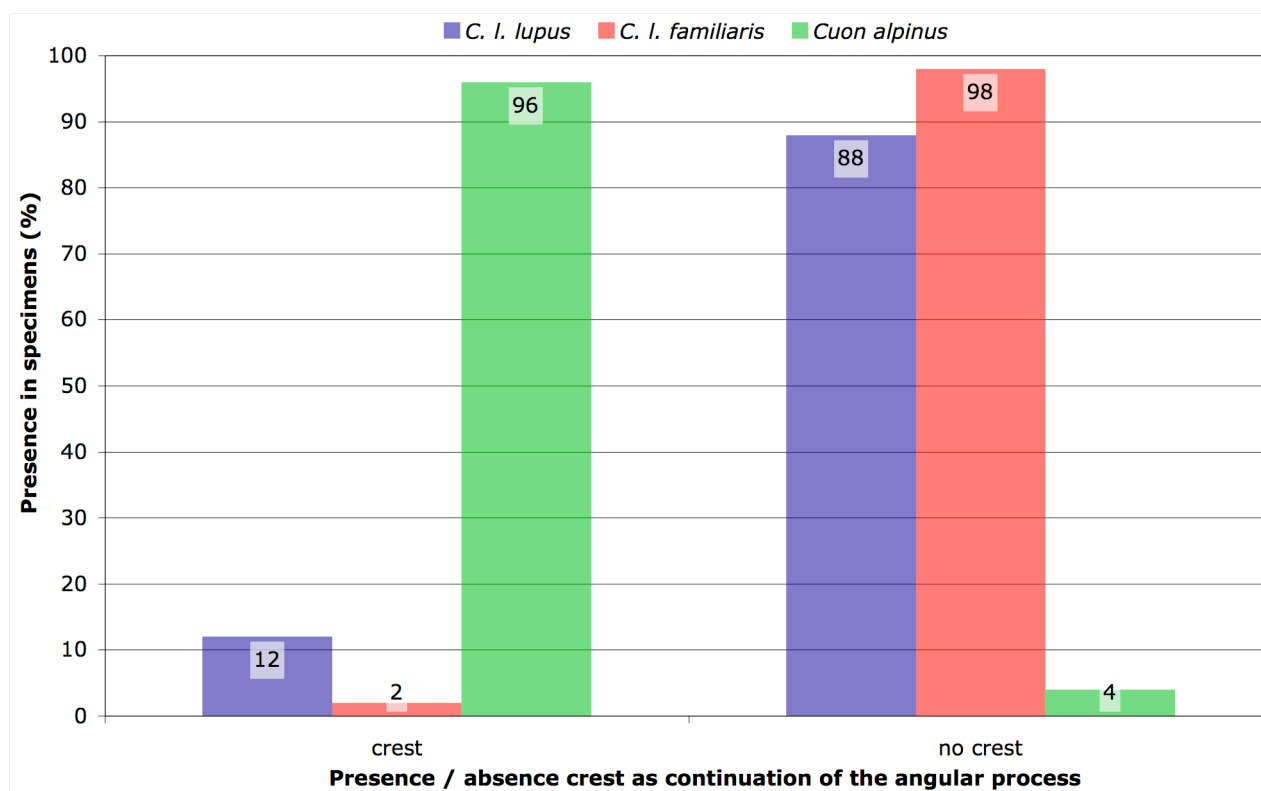
Another general morphological character of the mandibles of *Cuon alpinus* as compared to present-day *C. l. lupus* is that the angular process continues in a crest towards the masseteric fossa in *Cuon alpinus*, while this crest is absent or less marked in an oblique position in *C. l. lupus* (Pérez Ripoll et al., 2010, fig. IV.3). If results of the comparative material in this study also indicate this difference between the species, this parameter can be used to identify the fossil North Sea specimens.

### 4.3.5.1 Results comparative material

It was indeed observed that in *Cuon alpinus* specimens the angular process continues in a crest towards the masseteric fossa i.e. a distinct crest runs from the angular process towards the lower border of the masseteric fossa (appendix XIII). In *Canis* specimens this crest, if present at all, is much less marked and does not continue towards the masseteric fossa due to its often oblique position with respect to the mandibular body. In *Canis* there is thus a clear ‘flat’ part of the mandibular body between the angular process and the masseteric fossa, while in *Cuon alpinus* this part of the mandibular body is crossed by a distinct crest (as in fig. IV.3). Results thus coincide with those of Pérez Ripoll et al. (2010). Table 4.29 and fig. 4.24 show a summary the results of the comparative material (for all individual values of the comparative specimens, see appendix XIII). In most *Cuon alpinus* specimens (96%) the angular process continues in a crest and in most *Canis* specimens (98% and 88% for respectively *C. l. familiaris* and *C. l. lupus*) the crest is either absent or less marked; the results for these two genera are almost reversed (table 4.29). But this difference between *Cuon alpinus* and *Canis* is not entirely solid, since there also is one *Cuon alpinus* specimen in which the angular process does not continue in a crest and one *C. l. familiaris* specimen and two *C. l. lupus* specimens in which the angular process continues in a crest. There are no major differences between the two *Canis* species, although *C. l. lupus* is slightly more variable and shows a trend that is less strong than that observed in *C. l. familiaris*. The only *C. l. familiaris* specimen in which the angular process continues in a crest is a recent specimen from Suriname (appendix XIII).

**Table 4.29: Statistics of the parameter ‘Angular process’ of the comparative material (absolute counted specimens (#) and %).** The angular process can continue in a crest towards the masseteric fossa (crest) or the crest is either less marked in an oblique position or entirely absent (no crest). Sample sizes of the comparative (sub)species were: *C. l. lupus* (17), *C. l. familiaris* (42), *Cuon alpinus* (27).

Canidae material		Presence/absence crest as continuation of the angular process	
		crest	no crest
<i>C. l. lupus</i>	#	2	15
	%	12	88
<i>C. l. familiaris</i>	#	1	41
	%	2	98
<i>Cuon alpinus</i>	#	26	1
	%	96	4



**Figure 4.24:** Bar chart of the parameter 'Angular process' for the comparative material (in %). For each option is indicated how much percent of the specimens of the total sample sizes of the three comparative (sub)species were encountered with that option. For absolute counted specimens, sample sizes and the legend, see table 4.29.

#### 4.3.5.2 Results fossil North Sea material

See appendix I for photos of the 13 fossil North Sea specimens and the appearance of their angular processes compared to the typical *C. l. lupus* and *Cuon alpinus* appearances as depicted in fig. IV.3. See appendix XIII for the individual results of the specimens.

##### Specimens 534, 1683, 2196, 2620, 3219 and 3293

These fossil specimens do not have data for this parameter, because they either miss the entire posterior part of the mandible (ramus) or exactly the lower part of the mandibular body where the angular process can possibly continue in a crest (appendix I). For these six fossil North Sea specimens could not be determined what the appearance of the angular process was.

##### Specimens 535, 667, 2103, 2104, 2329, NMR89 and NMR90

These seven fossil North Sea specimens all have the typical *Canis* appearance of the angular process: the process is less marked than the typical *Cuon alpinus* process in some specimens and entirely absent in others (appendix I). Specimen 535 is a typical *Canis* example: there is a tiny edge in an oblique position that stops towards the masseteric fossa, where the mandibular body is flat (compare fig. IV.3 and fig. I.2). In this specimen the crest is much less marked than in *Cuon alpinus*. In specimen 667 the angular process is broken off exactly at the point where a possibly present crest would stop if it was less marked. If the angular process would have continued in a crest, this still could have been seen on this specimen. But the mandibular body between the process and masseteric fossa is quite flat, thus we can conclude that there was no pronounced crest like in *Cuon alpinus* (appendix I). Specimen 2103 possesses a little crest that is not really positioned in an oblique direction, but still stops towards the masseteric fossa, unlike *Cuon alpinus*. In specimens 2104, 2329 and NMR89 a crest is entirely absent and the mandibular body between the angular process and the masseteric fossa is flat. In specimen NMR90 the angular process is broken off and the lower mandibular body is partly missing, but the part of the mandible where a crest would be situated is still intact and clearly flat. Due to the missing angular process we cannot conclude whether a crest was completely absent or less marked, but NMR90 anyhow did not have a pronounced crest like *Cuon alpinus*.

### 4.3.6 Relation angular process - mandibular condyle (line k)

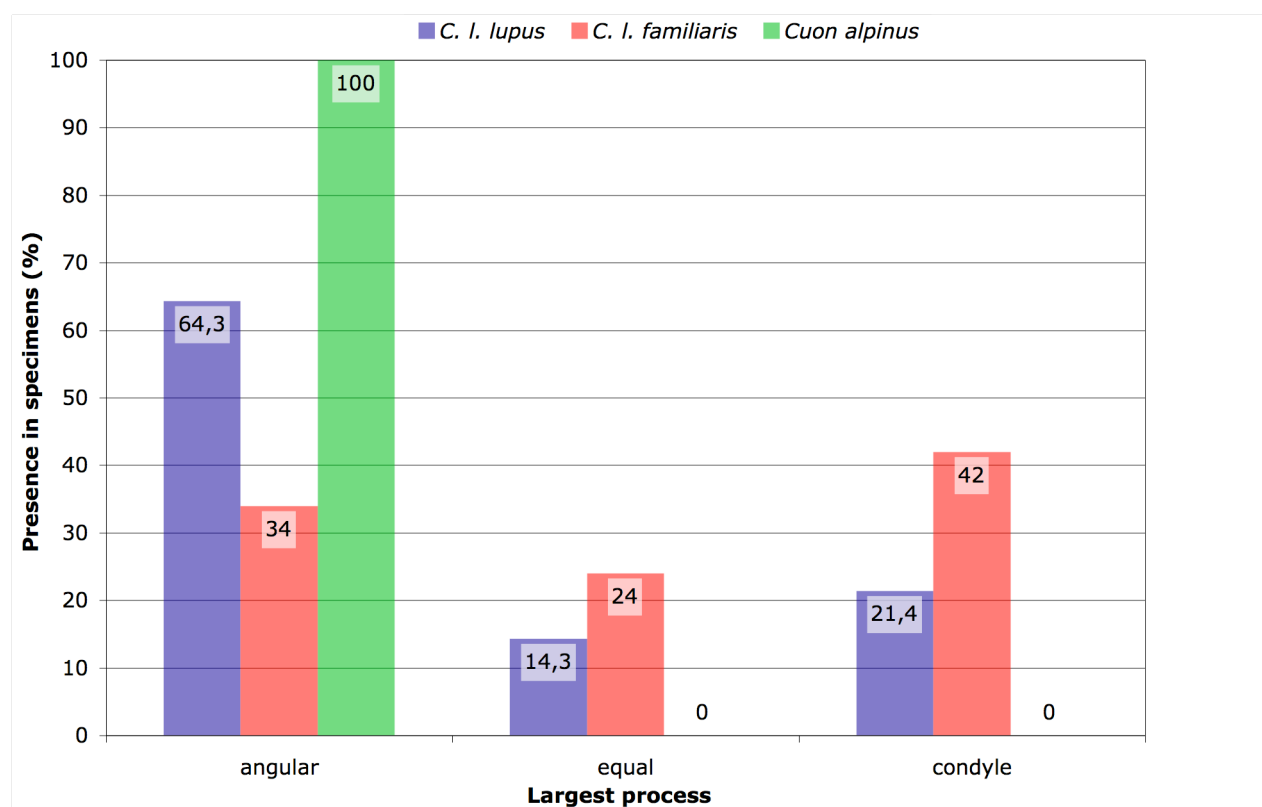
The last general morphological character of the mandibles of *Cuon alpinus* as compared to present-day *C. l. lupus* discussed in this section is that in *Cuon alpinus* the angular process is larger in the aboral direction compared to the mandibular condyle, while in *C. l. lupus* the process is shorter when compared to the condyle according to Pérez Ripoll et al. (2010) (fig. IV.3). But this comparative dataset shows another trend.

#### 4.3.6.1 Results comparative material

Table 4.30 and fig. 4.25 show a summary the results of the comparative material (for all individual values of the comparative specimens, see appendix XIII). For *Cuon alpinus* there is a very clear trend: in all comparative *Cuon alpinus* specimens the angular process is larger in the aboral direction than the mandibular condyle. Both *Canis* species are much more variable. In *C. l. familiaris* there is no clear trend in the relation between the angular process and the mandibular condyle: in most specimens (16) the mandibular condyle is larger in aboral direction, but in an almost equal amount of specimens (13) the angular process is larger and in many specimens these two protuberances of the ramus are equal in size (table 4.30). There are some differences between the recent material from Suriname and the fossil material from the Netherlands for this parameter (appendix XIII). In most recent specimens from Suriname the condyle is larger in the aboral direction than the angular process (55%), although there is also significant amount of specimens in which the angular process is larger (15%) or in which these two protuberances are equal in size (30%). In most fossil specimens from the Netherlands the angular process is larger than the condyle (56%), but also here there is a significant amount of specimens in which the condyle is larger (28%) or in which these two protuberances are equal in size (17%) (for absolute counted specimens, see appendix XIII). Like the fossil *C. l. familiaris* specimens from the Netherlands, *C. l. lupus* also shows a trend opposing the statements of Pérez Ripoll et al. (2010): the angular process is larger than the mandibular condyle in most specimens. There are also some specimens in which the angular process and mandibular condyle are equal in size and some in which the condyle is larger. Although *C. l. lupus* has a quite small sample size for this parameter (14 specimens), variation is still high.

**Table 4.30: Statistics of the parameter ‘Relation angular process – mandibular condyle’ of the comparative material (absolute counted specimens (#) and %).** The angular process can be larger (angular), shorter (condyle) or equal in size in the aboral direction compared to the mandibular condyle. Sample sizes of the comparative (sub)species were: *C. l. lupus* (14), *C. l. familiaris* (38), *Cuon alpinus* (27).

Canidae material		Largest process		
		angular	equal	condyle
<i>C. l. lupus</i>	#	9	2	3
	%	64,3	14,3	21,4
<i>C. l. familiaris</i>	#	13	9	16
	%	34	24	42
<i>Cuon alpinus</i>	#	27	-	-
	%	100	-	-



**Figure 4.25:** Bar chart of the parameter 'Relation angular process – mandibular condyle' for the comparative material (in %). For each option is indicated how much percent of the specimens of the total sample sizes of the three comparative (sub)species were encountered with that option. For absolute counted specimens, sample sizes and the legend, see table 4.30.

#### 4.3.6.2 Results fossil North Sea material

See appendix I for photos of the fossil North Sea specimens and appendix XIII for the relation of their angular process compared to the mandibular condyle. In most fossil North Sea specimens (534, 535, 667, 1683, 2196, 2620, 3219, 3293, NMR89 and NMR90) the ramus, angular process and mandibular condyle are partly eroded or entirely missing, thus this parameter could not be taken for these 10 fossil specimens (appendix I). In specimens 2103 and 2104 the angular process and mandibular condyle are equal in size in the aboral direction and in specimen 2329 the mandibular condyle is larger. In specimen 2104 the mandibular condyle actually seems to be slightly larger than the angular process on first sight, but we have to take into account that the angular process is slightly eroded. These seemingly larger condyle and the slight erosion of the angular process cancel each other out: the two protuberances were very likely equal in size. The angular process was certainly not larger than the mandibular condyle, because the amount of erosion of the angular process is not more than the amount by which the mandibular condyle seems to be larger (it can clearly be seen on specimen 2104 itself that only a tiny part of the process is eroded). In specimen 2329 the mandibular condyle is larger, but this is partly caused by the fact that the angular process is slightly eroded (again erosion is almost negligible). Originally the two protuberances were thus equal in size or the mandibular condyle was indeed larger (which is more probable), but the angular process was certainly not larger than the condyle (again the amount of erosion was not more than the amount by which the mandibular condyle seems to be larger).

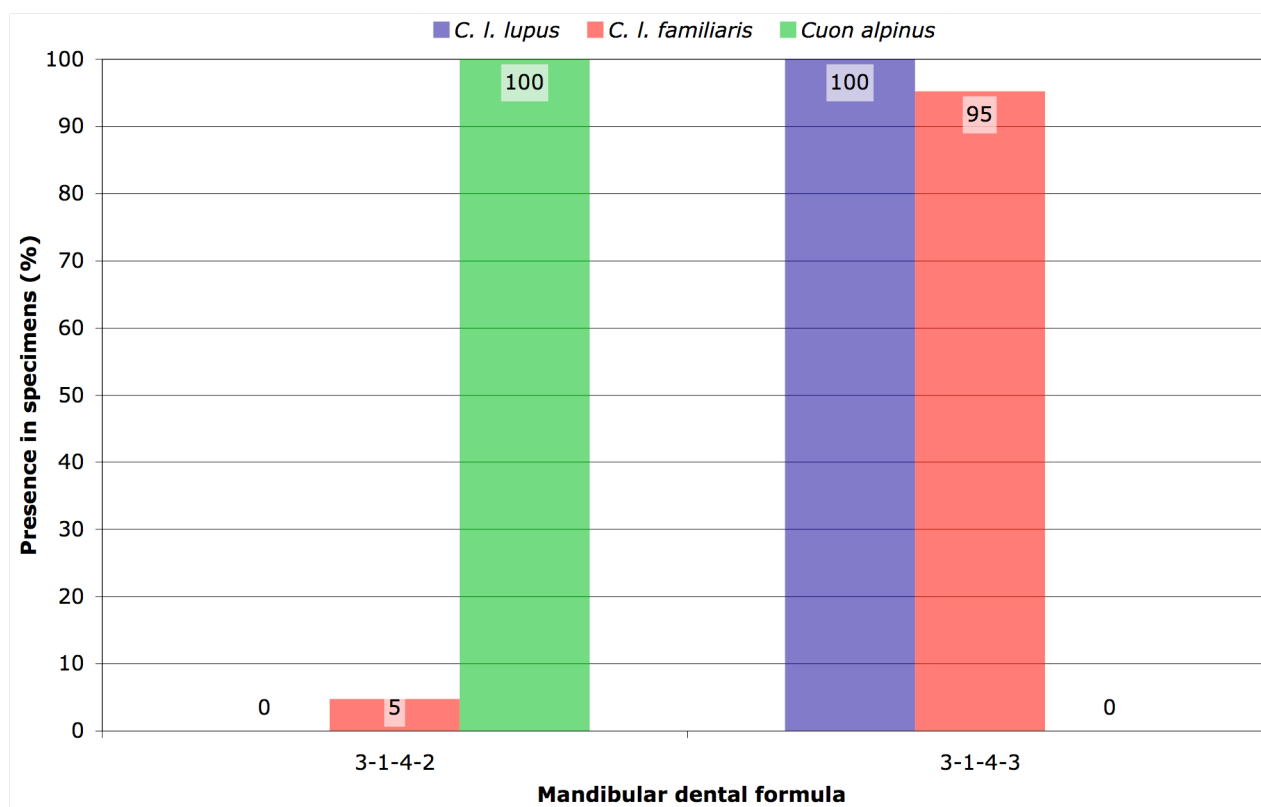
## 4.4 Teeth

### 4.4.1 Dental formula

The typical dental formula of Canidae is  $3/3-1/1-4/4-2/3$  (Durbin et al., 2008) (box III.1). This dental formula is relatively constant in the Canidae species (including *C. l. familiaris* and *C. l. lupus*), although some variation is possible; the Canidae dental formula can vary from  $3/3-1/1-4/4-2/3$  (42 teeth) to  $3/3-1/1-4/4-1/2$  (38 teeth), when the *Otocyon* (Bat-eared Fox), with its unusual dental formula of  $3/3-1/1-4/4-(3-4)/(4-5)$  (46-50 teeth), is ignored (Thenius, 1989). The genus *Cuon* has a unique (and constant) dentition within the Canidae family, with a dental formula of  $3/3-1/1-4/4-2/2$  (40 teeth) (Durbin et al., 2008). The difference between the typical dental formula of the two *Canis* species and *Cuon* is thus that *Cuon* only has two molars in its hemimandible ( $M_1$  and  $M_2$ ), while *C. l. familiaris* and *C. l. lupus* typically have three molars ( $M_1$ ,  $M_2$  and  $M_3$ ). In *Cuon* the  $M_3$  was reduced in time and eventually completely lost, while in the two *Canis* species the  $M_3$  is still present, although as small and round rudimentary tooth (Thenius, 1989). Taxonomic assignment to the genus *Cuon* is often partly based on this absence of a mandibular  $M_3$  (García and Arsuaga, 1998), but we also have to take into account that the dental formula of Canidae can vary and that in some Canidae species only two mandibular molars are present, as in *Cuon*. Results presented in this paragraph will show if variation in the dental formula also occurs in *C. l. lupus* and *C. l. familiaris* and if identification (on genus level) solely based on the mandibular dental formula is still possible. Since the 13 fossil North Sea specimens are only hemimandibles, only the results of the mandibular dental formula will be discussed into detail.

#### 4.4.1.1 Results comparative material

To see which dental formulas are possible in the three comparative species a record was kept of all teeth that are present, extra and missing (appendix XIII). When a tooth was missing, it was recorded whether an alveole, diastema or nothing was present instead of the tooth. These results can be found in appendix XI. In two *C. l. familiaris* specimens an extra teeth was observed: recent *C. l. familiaris* specimen 12547 is an adult specimen with an extra (left) maxillary premolar and recent *C. l. familiaris* specimen 18052 is an adult specimen with an extra (right) maxillary canine. But since these observations concern the maxilla, they will not be discussed any further. It was also observed in all comparative material that teeth were missing, but that an alveole or diastema was present instead i.e. in these cases we know that the missing tooth originally was or should have been present. Due to this missing tooth the dental formula is not different from the typical formula that is expected for that species and can be derived from the alveoles and/or teeth surrounding the diastema. More interesting were the two fossil *C. l. familiaris* specimens (hemimandibles 32044 and 74506) in which the  $M_3$  was missing and for which there was no alveole or diastema instead (appendices XI and XIII). There are thus no indications that the  $M_3$  originally was or should have been present and the mandibular dental formula of these two specimens is  $3-1-4-2$ , which is exactly the same as the mandibular dental formula of *Cuon* (fig. 4.26). When looking at the values of these two specimens for previous parameters, we see that 32044 and 74506 are average sized to small dogs that mostly fall within the *C. l. familiaris* and *Cuon alpinus* data clouds (mandible length, width and some parameters on the ramus, see graphs in corresponding paragraphs). For some parameters these *C. l. familiaris* specimens have typical *Canis* values (position of the foramina and the angular process), but for other parameters they have typical *Cuon* results (line k, crowded incisors) (appendix XIII). All remaining 38 *C. l. familiaris* specimens and all 18 *C. l. lupus* specimens have the typical Canidae dental formula ( $3-1-4-3$ ) in their mandible, thus including an  $M_3$ . (In all recent *Canis* specimens the typical Canidae formula was also observed in the maxilla.) All 27 *Cuon alpinus* specimens had the typical *Cuon* dental formula of  $3/3-1/1-4/4-2/2$  (appendix XIII). In this comparative dataset there are thus no *C. l. lupus* or *Cuon alpinus* specimens with a deviating dentition, on the contrary to *C. l. familiaris* (fig. 4.26).

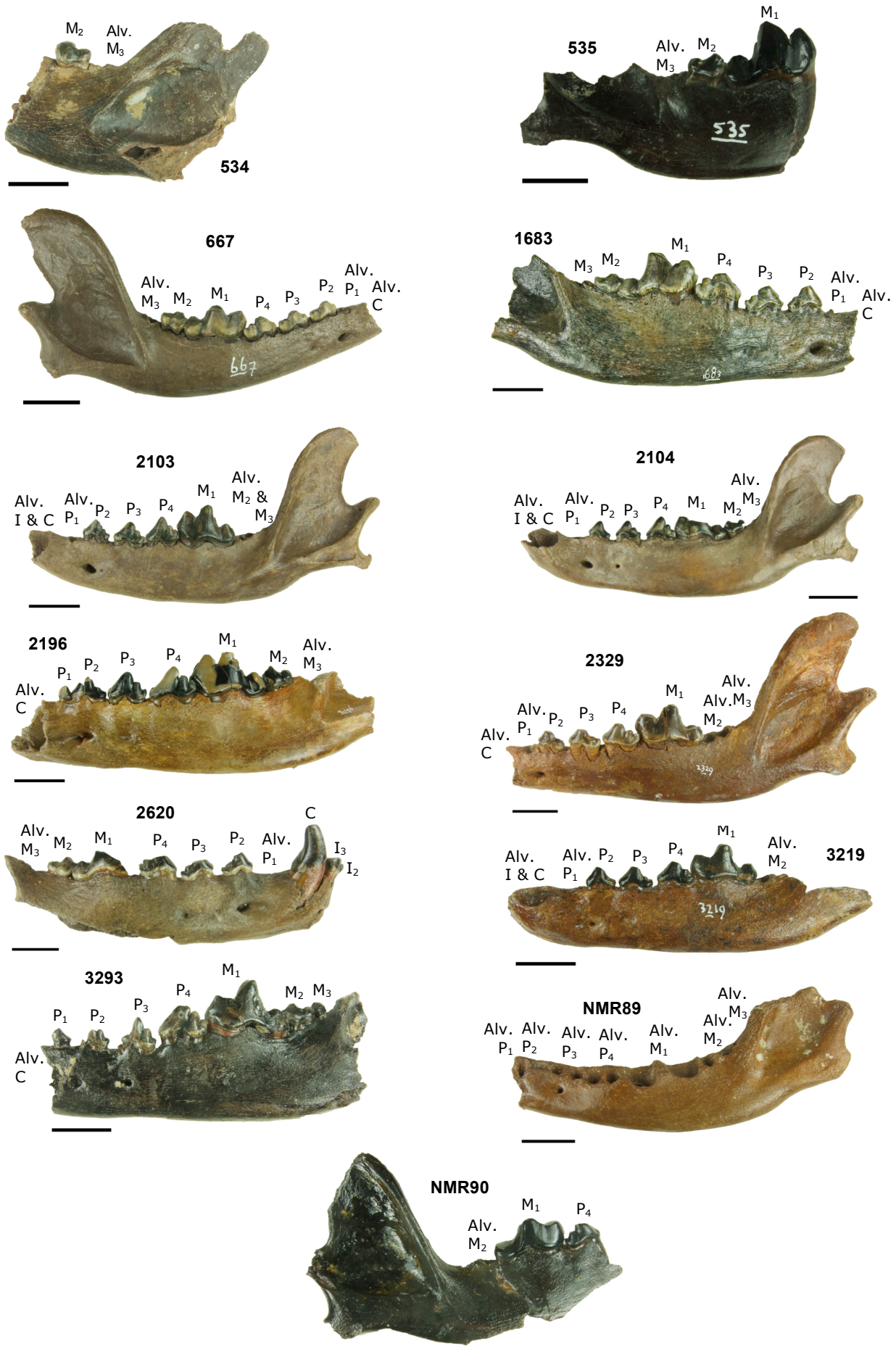


**Figure 4.26:** Bar chart of the parameter 'Mandibular dental formula' for the comparative material (in %). For each option (mandibular dental formula of 3-1-4-2 or 3-1-4-3) is indicated how much percent of the specimens of the total sample sizes of the three comparative (sub)species were encountered with that option. For absolute counted specimens and sample sizes see text above and appendix XIII.

#### 4.4.1.2 Results fossil North Sea material

For all dental formula's in the 13 fossil specimen see plate 4.1 and appendix XIII, for larger images of the fossils specimens see appendix I. Specimens 534 and 535 are posterior parts of a hemimandible in which the  $M_2$  (for 534) and  $M_2$  and  $M_1$  (for 535) are still present, but in which the  $M_3$  is absent. In specimens 667, 2103, 2104, 2196, 2329, 2620 and NMR89 a larger part of the original tooth row is still present, but the  $M_3$  also misses. However, a clear small, round alveole of an  $M_3$  can be seen in all these specimens, thus an  $M_3$  was originally present; these specimens have the typical Canidae dental formula. In specimens 1683 and 3293 even a small rudimentary  $M_3$  is still present, thus these two specimens also have the typical Canidae dental formula. In specimen 3219 the posterior part of the mandible is broken off exactly behind the distal alveole of  $M_2$ , thus the dental formula could not be determined for this specimen. In NMR90 the  $M_3$  is absent and an alveole or diastema instead of the tooth are neither present: the anterior border of the ramus starts immediately posterior of the posterior alveole of  $M_2$  as in *Cuon alpinus* specimens and the two *C. l. familiaris* specimens with deviating dental formula. The mandibular dental formula of NMR90 is thus 3-1-4-2.

**Plate 4.1: The 13 fossil North Sea specimens with indication of teeth that are present or alveoles of teeth that were originally present in the specimen. Bold number is the specimen reg. no. Scale bar: 2 cm. For larger images of the fossil specimens, see appendix I. See box III.1 and IV.4 for an explanation of the dental formula.**





## 4.4.2 Height of the crown of (P<sub>1</sub>), P<sub>4</sub> and M<sub>1</sub>

In *Cuon alpinus* the premolars have relatively higher crowns and are more sharp-pointed than in *Canis* (García and Arsuaga (1998) and Thenius (1989)). The P<sub>1</sub> in particular is better developed (considerably larger) in *Cuon alpinus*, probably due to the fact that this tooth is more functional in *Cuon alpinus* than in *Canis* (Pérez Ripoll et al., 2010); in *Cuon alpinus* the first premolars come in contact at closure of the jaws and play a role in the grabbing teeth set, but this is not the case in *Canis* (Thenius 1989). On the other hand, molars would be clearly larger in *Canis* (Pérez Ripoll et al., 2010). The heights of the crowns of premolars and molars can thus be used to identify the 13 fossil North Sea specimens. Therefore, the heights of the crowns of the P<sub>1</sub>, P<sub>4</sub> and M<sub>1</sub> were measured. Since only two fossil North Sea specimens have values for P<sub>1</sub>, these results will not be discussed extensively. Results for P<sub>4</sub> and M<sub>1</sub> will be discussed in more detail.

### 4.4.2.1 Height of the crown of P<sub>1</sub>

The two fossil North Sea specimens in which a P<sub>1</sub> is still present are specimens 2196 and 3293 (plate 4.1). The P<sub>1</sub> of these specimens qualitatively do not have a typical *Cuon alpinus* or *Canis* appearance: they are not flat as in *Canis*, but neither high, sharp-pointed and more conical as in *Cuon alpinus* (appendix XIII). The quantitative evidence of the height of the crown is also inconclusive: analysis of the results of the comparative material and specimens 2196 and 3293 revealed that the specimen ranges of both specimens fall in all sample and population ranges of all three comparative species (table X.3). Since this parameter is not indicative about the identity of the fossil North Sea specimens it will not be discussed any further.

### 4.4.2.2 Height of the crown of P<sub>4</sub> and M<sub>1</sub>

#### 4.4.2.2a Results comparative material

For all values mentioned below see both table 4.31 and fig. 4.27 unless stated otherwise.

**x** With 9.86 mm *C. l. lupus* has on average the biggest crown height for P<sub>4</sub>, followed by *Cuon alpinus* (8.29 mm) and *C. l. familiaris* (7.71 mm). Values are larger for the crown height of M<sub>1</sub> but the trend is the same: *C. l. lupus* has clearly the highest crowns and the average values for *Cuon alpinus* and *C. l. familiaris* are lower and lie closer together, although for this parameter *Cuon alpinus* has higher values than *C. l. familiaris*.

**SD vs. n** Also for this parameter *C. l. lupus* has the smallest sample size (even much smaller than in previous parameters, with only 13 specimens for P<sub>4</sub>), but the largest variation (SD of 1.50 mm for P<sub>4</sub>) (table 4.31). In many fossil *C. l. familiaris* specimens the height of the crown could not be measured, due to erosion of teeth and missing teeth (plate 4.1). As a result the sample sizes of *Cuon alpinus* and *C. l. familiaris* lies very close together for this parameter (27 respectively 30 for P<sub>4</sub>), but the sample size of *C. l. familiaris* is still slightly larger. Variation in the *C. l. familiaris* dataset is also larger than the variation in *Cuon alpinus* (SDs of respectively 0.94 and 0.55 mm for P<sub>4</sub>), but more than would be expected proportionally to the only slightly larger sample size (table 4.31). Also for this parameter variation in values for *Cuon alpinus* is (extremely) low compared to the two *Canis* species. Values are similar for M<sub>1</sub> and the same peculiar trend can be seen.

**Sample ranges:** see table 4.31. For both M<sub>1</sub> and P<sub>4</sub> the *Cuon alpinus* sample range falls (almost) entirely within both *Canis* ranges; only for M<sub>1</sub> the *Cuon alpinus* minimum is slightly (0.33 mm) lower than the *C. l. lupus* minimum. This high amount of overlap with *C. l. lupus* is partly caused by the relative higher premolar crowns of *Cuon alpinus* compared to this species; the *C. l. lupus* data cloud is shifted towards the left of fig. 4.27 (lower P<sub>4</sub> or higher M<sub>1</sub> crown heights) relative to *Cuon alpinus* and *C. l. familiaris*. *C. l. familiaris* occupies the lowermost part of fig. 3.31 and *C. l. lupus* the uppermost part (since the *C. l. familiaris* and *Cuon alpinus* maxima are lower than the *C. l. lupus* mean), but overlap between the three comparative species is great. Also for this parameter a distinction can be made within the *C. l. familiaris* group, separating the fossil specimens from the Netherlands from the recent specimens from Suriname (fig. VII.9). Most recent specimens plot below the *C. l. familiaris* mean, although there are also some specimens that plot in the upper part of the *C. l. familiaris* range. The fossil specimens from the Netherlands mostly plot above the *C. l. familiaris* mean. For this parameter the data points of all comparative species plot evenly over their ranges in a quite linear way; there are no remarkable specimens that have an extremely low or high value for M<sub>1</sub> in proportion to P<sub>4</sub> compared to other specimens of its species (fig. 4.27).

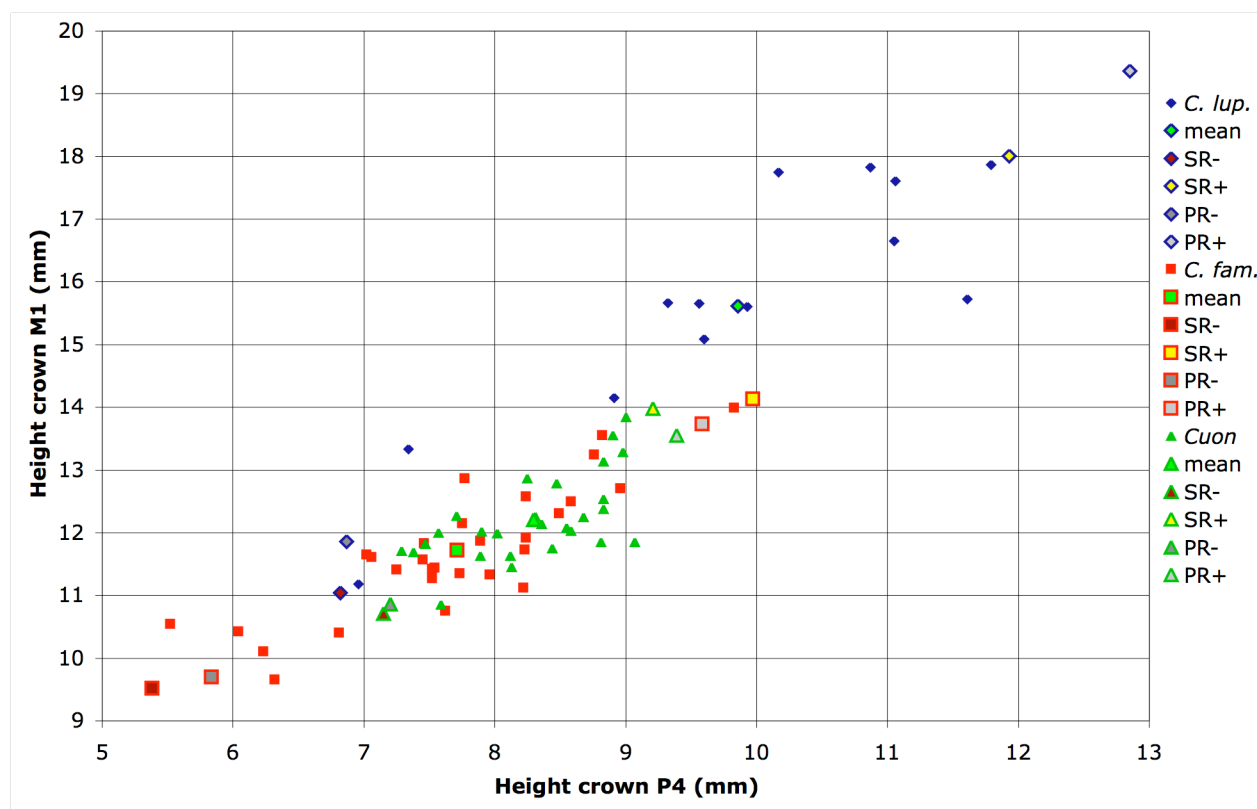
**Population ranges:** see table 4.31. For the population ranges there is still much overlap between the comparative species. The *Cuon alpinus* range falls entirely within both *Canis* ranges for P<sub>4</sub>, also within the *C. l. familiaris* for M<sub>1</sub> and only slightly below the *C. l. lupus* minimum for M<sub>1</sub>. Also for the population ranges *C. l. familiaris* occupies the lowermost part of fig. 4.27 and *C. l. lupus* the uppermost part (since the *C. l. familiaris* and *Cuon alpinus* maxima are lower than the *C. l. lupus* mean).

**Trend lines** All three comparative species have slightly more variation in the crown height of M<sub>1</sub> than in P<sub>4</sub> (table 4.31 and the axes of fig. 4.27), but in general the two parameters are quite similar and data points plot on a nice linear line: parameters P<sub>4</sub> and M<sub>1</sub> are well comparable. A prominent feature in fig. 4.27 is that *C. l. lupus* specimens mostly are positioned 'above' *C. l. familiaris* and *Cuon alpinus* specimens; for a fixed value of M<sub>1</sub> *C. l. lupus* specimens have a lower value for P<sub>4</sub> than *C. l. familiaris* and *Cuon alpinus* (the trend line of

*C. l. lupus* is shifted towards the left (lower premolar crown heights) compared to *C. l. familiaris* and *Cuon alpinus* in fig. VIII.4). This proportional difference between the crown height of P<sub>4</sub> and M<sub>1</sub> can be an aid in the identification of the fossil North Sea specimens.

**Table 4.31: Statistics of the parameters 'Height of the crown' P<sub>4</sub> (left) and M<sub>1</sub> (right) of the comparative material (in mm).** Legend: see table 4.1.

Statistics	Height of the crown of P <sub>4</sub>			Height of the crown of M <sub>1</sub>		
	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>
Sample size (n)	13	30	27	17	32	27
Sample mean (x)	9,86	7,71	8,29	15,61	11,7	12,21
Standard deviation (SD)	1,50	0,94	0,55	1,88	1,01	0,67
Minimum (MIN)	6,96	5,52	7,29	11,18	9,66	10,85
Maximum (MAX)	11,8	9,83	9,07	17,87	14,0	13,84
Sample range MIN	6,82	5,38	7,15	11,04	9,52	10,71
Sample range MAX	11,9	9,97	9,21	18,01	14,1	13,98
Population range MIN	6,87	5,84	7,20	11,86	9,70	10,86
Population range MAX	12,9	9,58	9,39	19,37	13,7	13,56



**Figure 4.27: Scatter plot of parameters 'Height of the crown' P<sub>4</sub> vs. M<sub>1</sub> for the comparative material (in mm).** Legend, see table 4.1.

#### 4.4.2.2b Results fossil North Sea material

Not all 13 fossil North Sea specimens had values for both parameters, thus only 8 specimens could be plotted in fig. 4.28. For 7 of the 10 fossil North Sea specimens that have a value for the P<sub>4</sub> or M<sub>1</sub> crown height or both, the P<sub>4</sub> and/or M<sub>1</sub> was slightly eroded, thus the exact crown height could not be measured (appendix I). But in all of these specimens the tooth in question was only slightly eroded and a sufficient part of the cusps remained to make a reasonable estimate of the original height of the crown. Values that are given for these specimens are 'lower boundary' estimates: the value indicates the minimum height of the crown of the tooth. Thus keep in mind that for some of the following fossil North Sea specimens the specimen ranges are estimates.

### Specimens 534, 2620 and NMR89

In these three fossil North Sea specimens the  $P_4$  and  $M_1$  are not present (534 and NMR89) or highly eroded (2620), thus the height of the crown cannot be measured or estimated (appendix I).

### Specimen 535

Specimen 535 only has values for  $M_1$  (due to a missing  $P_4$ ) and as a result could not be plotted in fig. 4.28. The  $M_1$  is still intact and not eroded, thus the values were exactly measured and not estimated for this specimen. The specimen range of 535 falls entirely within the sample and population ranges of *C. l. lupus* and entirely outside the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* (table 4.32 and fig. 4.28). The mean value of specimen 535 for  $M_1$  (17.78 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 2.17 mm between the two mean values) and much less similar to the average *Cuon alpinus* and *C. l. familiaris* specimen (with 5.57 and 6.06 mm respectively) (appendix XIII).

### Specimens 667, 2103, 2104 and NMR90

Values for specimens 667 and NMR90 were estimated, because the cusps of the  $M_1$  and  $P_4$  are slightly eroded (appendix I). The  $M_1$  of specimen 2104 is highly eroded and could not be measured or estimated, but the height of the crown of the  $P_4$  of 2104 and both teeth of specimen 2103 were exactly measured. The specimen ranges of these four specimens fall in the sample and population ranges of all three comparative species (table 4.32 and fig. 4.28). Values for specimens 667 and NMR90 were estimated ('lower boundary' values), but even if the values would have been slightly larger, the specimen ranges still would fall within all comparative ranges (fossil part of the *C. l. familiaris* sample range, fig. VII.9), as can clearly be seen from the position of these specimens in fig. 4.28. Mean values of specimen 667 and NMR90 are neither indicative for the identity of these specimens: the mean value of these specimens is most similar to the average *C. l. familiaris* for  $P_4$  and most similar to the average *Cuon alpinus* for  $M_1$ . Mean values of specimens 2103 and 2104 indicate that these specimens are more similar to the average *Cuon alpinus* specimen than to the two *Canis* species (appendix XIII). Specimens 667 and NMR90 plot in the middle of the *C. l. lupus* trend line and those of *C. l. familiaris* and *Cuon alpinus* and specimen 2103 plots closer to the trend lines of *C. l. familiaris* and *Cuon alpinus*, but neither of the three specimens has a particularly high crown of its  $M_1$  in proportion to its  $P_4$  crown height compared to other *C. l. familiaris* and *Cuon alpinus* specimens (fig. VIII.4). Specimen 2104 was not plotted in fig. 4.28, due to its missing value for  $P_4$ .

### Specimen 1683

Values for the  $P_4$  and  $M_1$  of 1683 were estimated due to slight erosion of the cusps of these both teeth. The specimen range falls entirely outside (far above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* and inside the sample and population ranges of *C. l. lupus* (table 4.32 and fig. 4.28). Specimen 1683 has quite high crowns and even falls partly outside (above) the *C. l. lupus* sample range for  $M_1$  (as is clearly seen in fig. 3.32). The mean value of specimen 1683 for  $P_4$  (11.48 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 1.98 mm between the two mean values) and much less similar to the average *Cuon alpinus* and *C. l. familiaris* specimen (with 3.55 and 4.13 mm respectively) (appendix XIII). This trend is the same for  $M_1$ . Specimen 1683 plots exactly on the *C. l. lupus* trend line, which indicates that the height of the crown of the  $M_1$  is quite high in proportion to the crown height of  $P_4$  in comparison to *Cuon alpinus* and *C. l. familiaris* specimens (fig. VIII.4).

### Specimen 2196

Values for the  $P_4$  of this specimen were exactly measured, but for the  $M_1$  they were estimated due to slight erosion of this tooth. The specimen range of 2196 falls entirely outside (above) the sample and population ranges of *Cuon alpinus* and *C. l. familiaris*, but entirely inside both *C. l. lupus* ranges (table 4.32). As is clearly seen in fig. 4.28, the mean value of specimen 2196 for  $P_4$  (10.87 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 1.01 mm between the two mean values) and much less similar to the average *Cuon alpinus* and *C. l. familiaris* specimen (with 2.58 and 3.16 mm respectively). This trend is the same for  $M_1$ . In fig. VIII.4 specimen 2196 is positioned above the *C. l. lupus* trend line, which means that in this specimen the height of the crown of  $M_1$  is clearly larger proportionally to the crown height of  $P_4$ .

### Specimen 2329

In this specimen the crown heights of  $P_4$  and  $M_1$  are both estimated due to slight erosion of the cusps of these teeth. The specimen range of 2329 falls entirely outside (above) the sample and population ranges of *Cuon alpinus* and *C. l. familiaris*, but entirely inside both *C. l. lupus* ranges (table 4.32). As is clearly seen in fig. 4.28, the mean value of specimen 2329 for  $P_4$  (10.35 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.49 mm between the two mean values) and much less similar to the average *Cuon alpinus* and *C. l. familiaris* specimen (with 2.06 and 2.64 mm respectively). This trend is the same for  $M_1$ . Specimen 2329 plots slightly below the *C. l. lupus* trend line, but the height of the crown of  $M_1$  is still proportionally larger than the crown height of  $P_4$  compared to *Cuon alpinus* and *C. l. familiaris* specimens (fig. VIII.4).

### Specimen 3219

In this specimen the crown heights of P<sub>4</sub> and M<sub>1</sub> are both estimated due to slight erosion of the cusps of these teeth. The specimen range of 3219 falls within the sample and population ranges of all three comparative species for P<sub>4</sub> and within the *C. l. lupus* sample and population ranges for M<sub>1</sub> (table 4.32 and fig. 4.28). 3219 Only slightly overlaps with the upper part of the *C. l. familiaris* and *Cuon alpinus* sample ranges and falls entirely outside (above) corresponding population ranges. Due to its position in the middle of fig. 4.28 results for the mean values of this specimen are quite random: the mean value of specimen 3219 for P<sub>4</sub> is most similar to the average *Cuon alpinus* specimen, less similar to the average *C. l. familiaris* specimen and least similar to the average *C. l. lupus* specimen, but the mean value of specimen 3219 for M<sub>1</sub> is most similar to the average *C. l. lupus* specimen, less similar to the average *Cuon alpinus* specimen and least similar to the average *C. l. familiaris* specimen (appendix XIII). Specimen 3219 is plotted close to the *C. l. lupus* trend line, but not far above the *C. l. familiaris* and *Cuon alpinus* data clouds (fig. VIII.4).

### Specimen 3293

The crown height of P<sub>4</sub> was estimated due to very slight erosion of the main cusp of this tooth, but M<sub>1</sub> could be measured exactly. Specimen 3293 falls entirely outside (far above) the sample and population ranges of *Cuon alpinus* and *C. l. familiaris* and entirely inside (in the upper part of) the *C. l. lupus* sample and population ranges for both teeth (table 4.32). As is clearly seen in fig. 4.28, the mean value of specimen 3293 for P<sub>4</sub> (11.72 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 1.86 mm between the two mean values) and much less similar to the average *Cuon alpinus* and *C. l. familiaris* specimen (with 3.43 and 4.01 mm respectively). This trend is the same for M<sub>1</sub>. This specimen plots between the trend lines of *C. l. lupus* and *C. l. familiaris* and *Cuon alpinus* and does not have a particular high molar crown in proportion to its fourth premolar crown (fig. VIII.4).

**Table 4.32: Comparison of the specimen ranges of the fossil North Sea specimens with the sample and population ranges of the comparative material for parameters ‘Height crown’ P<sub>4</sub> (left) and M<sub>1</sub> (right) (in mm).** Sample and population ranges of the comparative material are as given in table 4.31. Specimen ranges were calculated as explained in table 4.2.

Canidae material		Height of the crown of P <sub>4</sub>				Height of the crown of M <sub>1</sub>			
		- Sample range +		- Population range +		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	6,82	11,9	6,87	12,9	11,04	18,01	11,86	19,37
	<i>C. l. familiaris</i>	5,38	9,97	5,84	9,58	9,52	14,1	9,70	13,7
	<i>Cuon alpinus</i>	7,15	9,21	7,20	9,39	10,71	13,98	10,86	13,56
Fossil North Sea	535	-	-	-	-	17,64	17,92	-	-
	667	7,75	8,03	-	-	12,48	12,76	-	-
	1683	11,70	11,98	-	-	17,98	18,26	-	-
	2103	8,90	9,18	-	-	13,07	13,35	-	-
	2104	7,98	8,26	-	-	-	-	-	-
	2196	10,73	11,01	-	-	17,29	17,57	-	-
	2329	10,21	10,49	-	-	15,34	15,62	-	-
	3219	8,50	8,78	-	-	13,93	14,21	-	-
	3293	11,58	11,86	-	-	16,7	16,98	-	-
NMR90	7,36	7,64	-	-	11,99	12,27	-	-	

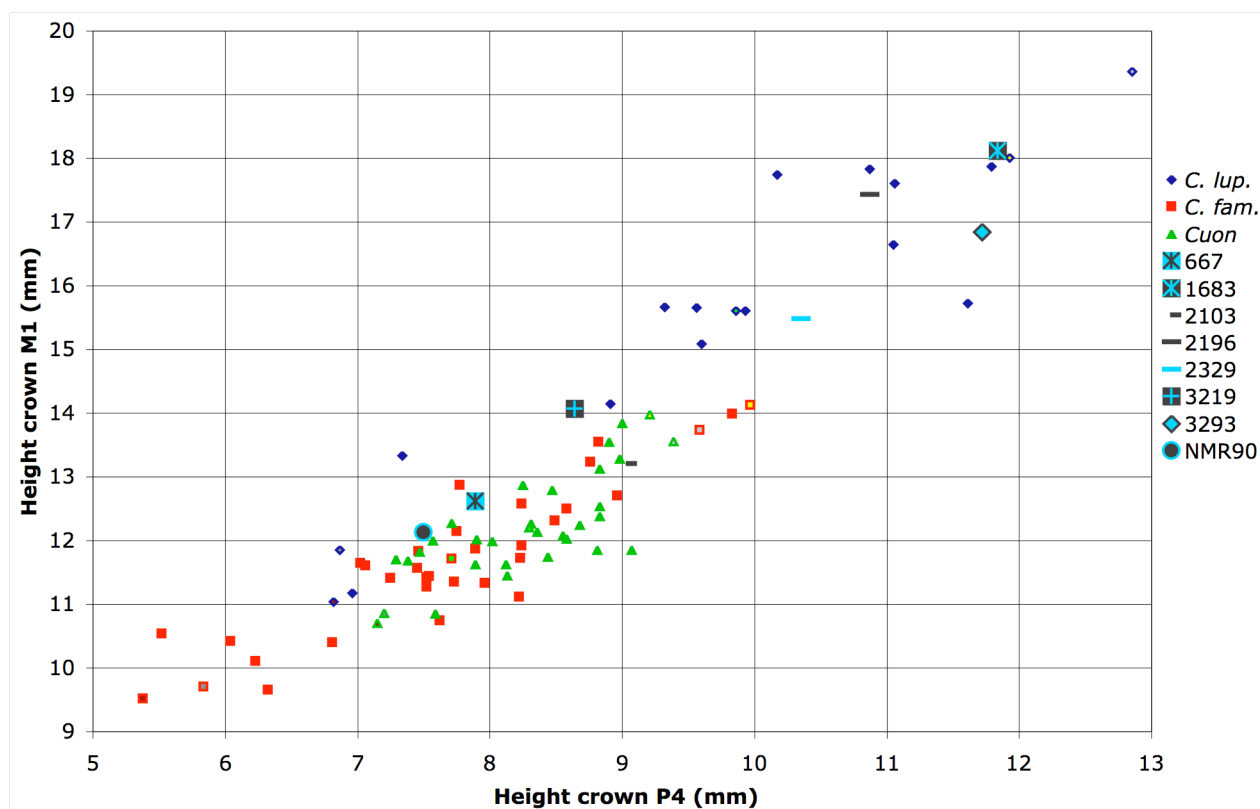


Figure 4.28: Scatter plot of parameters 'Height crown' P<sub>4</sub> vs. M<sub>1</sub> for the fossil North Sea specimens and the comparative material (in mm). Legend, see tables 4.1 and 4.2.

### 4.4.3 Length and breadth of M<sub>1</sub> and M<sub>2</sub>

As was observed in the parameter 'Height of the crown' the premolars of *Cuon alpinus* and *C. l. familiaris* were relatively higher than the premolars of *C. l. lupus*, but the absolute values of *Cuon alpinus* and *C. l. familiaris* lay close together. It is indeed known that the front teeth of Carnivora are far more uniform than the back teeth and that differentiation of teeth mainly occurs in molars (Thenius, 1989). Greater differences are thus expected between the molars of the three comparative species than between the premolars; in *Canis* molars would have clearly larger dimensions than in *Cuon alpinus* (Pérez Ripoll et al., 2010). Therefore only the first two molars were measured for the parameter 'Length and breadth of the tooth'.

#### 4.4.3.1 Length and breadth of M<sub>1</sub>

##### 4.4.3.1a Results comparative material

For all values mentioned below see both table 4.33 and fig. 4.29 unless stated otherwise.

**x** With 27.19 mm *C. l. lupus* has on average the biggest length for M<sub>1</sub>, followed by *C. l. familiaris* (21.25 mm) and *Cuon alpinus* (20.49 mm). Values are smaller for the breadth of M<sub>1</sub> but the trend is the same: *C. l. lupus* has clearly the widest molars and the average values for *Cuon alpinus* and *C. l. familiaris* are lower and lie closer together (table 4.33).

**SD vs. n** For the length *C. l. lupus* has the smallest sample size (18), but the largest variation (SD of 2.20 mm). *C. l. familiaris* has a much larger sample size (38), but the variation is almost as large (SD of 2.13). For the breadth *C. l. familiaris* has the largest sample size and also the largest variation, but the standard deviation of *C. l. lupus* is not much smaller than that of *C. l. familiaris* while its sample size is (table 4.33). For both parameters *Cuon alpinus* is again the species with the lowest variation, while its sample size is quite large.

**Sample ranges:** see table 4.33. For both parameters there is some, but not much, overlap between the *Cuon alpinus* and *C. l. lupus* ranges and the *Cuon alpinus* range falls entirely within the *C. l. familiaris* range. *C. l. familiaris* has a large range that plots from below the *Cuon alpinus* minimum to well within the *C. l. lupus* range (fig. 4.29). For this parameter again a distinction can be made within the *C. l. familiaris* group, separating the fossil specimens from the Netherlands from the recent specimens from Suriname. As for previous parameters recent specimens plot over the entire *C. l. familiaris* range, while the fossil specimens are concentrated in the upper part of the *C. l. familiaris* range (fig. VII.10). For this parameter the data points of all comparative species plot evenly over their ranges in a quite linear way; there are no remarkable

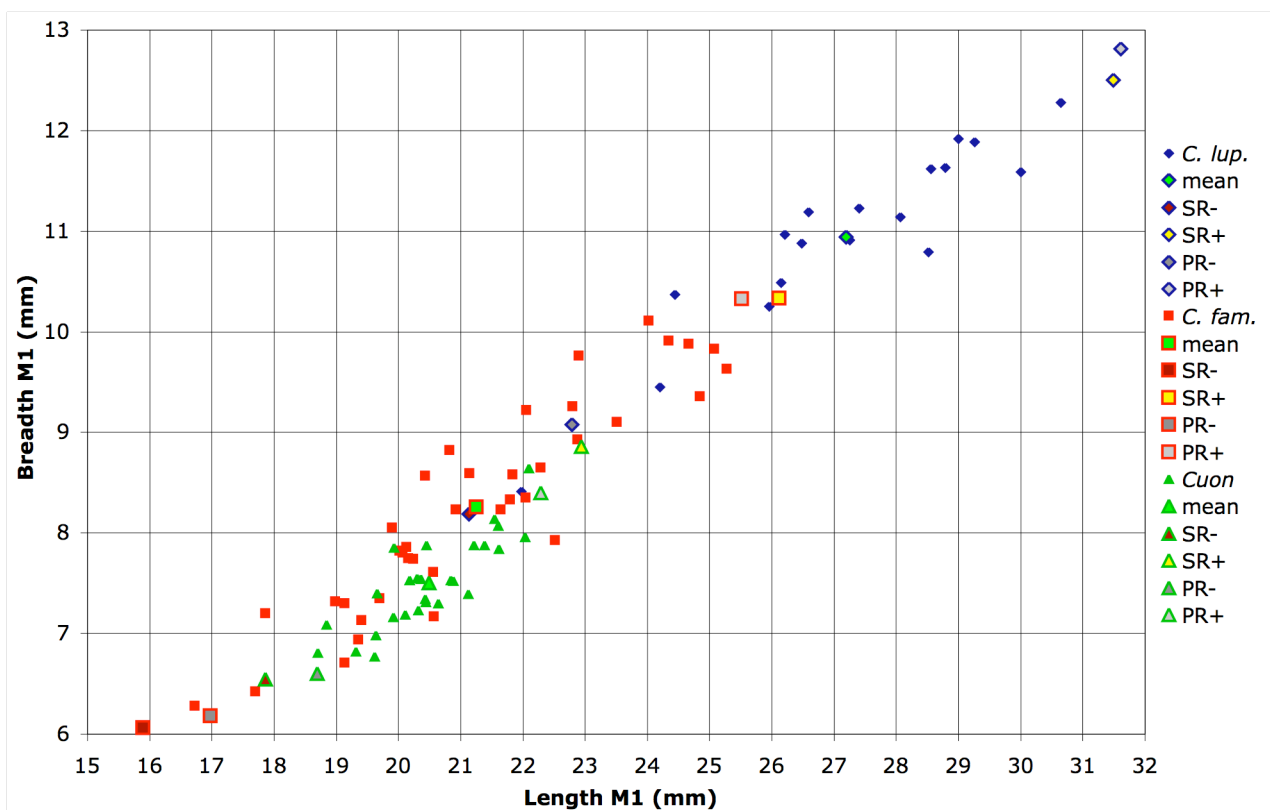
specimens that have an extremely low or high value for the breadth of  $M_1$  in proportion to the length (fig. 4.29). However, the overlap between the *C. l. lupus* and *Cuon alpinus* ranges is caused by specimen *lupus-m*, which is the only *C. l. lupus* specimen that plot within the *Cuon alpinus* range and is quite small compared to the other *C. l. lupus* specimens.

**Population ranges:** see table 4.33. For these ranges *Cuon alpinus* and *C. l. lupus* are nicely separated; for both parameters the *Cuon alpinus* maximum  $M_1$  length and breadth that were encountered in this comparative dataset are smaller than the *C. l. lupus* minimum. *C. l. familiaris* still overlaps greatly with these both species.

**Trend lines** All three comparative species have slightly more variation in the length of  $M_1$  than in the breadth, but in general the two parameters are quite similar and data points plot on a nice linear line: the length and breadth of  $M_1$  are well comparable. There are some slight differences between the positions of the trend lines (if plotted) of the three comparative species, but all three trend lines fall within the 'bandwidth' of all three data clouds. Trend lines would thus not be an aid in the identification of the fossil North Sea specimens and are not given or discussed.

**Table 4.33: Statistics of the parameters 'Length' (left) and 'Breadth' (right) of  $M_1$  of the comparative material (in mm).** Legend: see table 4.1.

Statistics	Length $M_1$			Breadth $M_1$		
	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>
Sample size (n)	18	38	27	18	38	27
Sample mean (x)	27,19	21,25	20,49	10,9	8,26	7,50
Standard deviation (SD)	2,20	2,13	0,90	0,93	1,04	0,45
Minimum (MIN)	21,97	16,73	18,70	8,41	6,28	6,77
Maximum (MAX)	30,65	25,28	22,10	12,3	10,1	8,64
Sample range MIN	21,13	15,89	17,86	8,19	6,06	6,55
Sample range MAX	31,49	26,12	22,94	12,5	10,3	8,86
Population range MIN	22,79	16,98	18,69	9,08	6,18	6,61
Population range MAX	31,60	25,52	22,28	12,8	10,3	8,40



**Figure 4.29: Scatter plot of parameters 'Length' vs. 'Breadth' of  $M_1$  for the comparative material (in mm).** Legend, see table 4.1.

#### 4.4.3.1b Results fossil North Sea material

Not all 13 fossil North Sea specimens had values for both parameters, thus only 10 specimens could be plotted in fig. 4.30.

##### Specimens 534 and NMR89

The  $M_1$  is not present in these two fossil North specimens (plate 4.1), thus no data are available.

##### Specimen 535

The specimen range of 535 falls entirely outside (far above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* and entirely within the *C. l. lupus* ranges, as clearly can be seen in fig. 4.30. The mean value of specimen 535 for the length (28.03 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.84 mm between the two mean values) and much less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 6.78 and 7.54 mm respectively) (appendix XIII). This trend is the same for the breadth.

##### Specimen 667

This specimen falls entirely within the (fossil part of the) *C. l. familiaris* sample and population ranges for the length and breadth and within the *Cuon alpinus* sample and population ranges for the length of  $M_1$  (table 4.34, fig. 4.30 and fig. VII.10). 667 Also falls within the *Cuon alpinus* sample range for the breadth, but partly outside (above) the corresponding population range. This specimen falls partly outside (below) the *C. l. lupus* sample ranges and entirely outside the population ranges for both the length and breadth of  $M_1$ . The mean value of specimen 667 for the length (20.03 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.32 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 0.44 mm) and most dissimilar to the average *C. l. lupus* specimen (with 6.26 mm) (see appendix XIII for the mean values). This trend is the same for the breadth.

##### Specimen 1683

The specimen range of 1683 falls entirely outside (far above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* and within the *C. l. lupus* sample and population ranges (table 4.34 and fig. 4.30). 1683 Even falls partly outside (above) the *C. l. lupus* sample range for the breadth of  $M_1$ . The large dimensions of this specimen are obvious from fig. 4.30 and the fact that the mean value of 1683 for the length (30.12 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 2.93 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 8.87 and 9.63 mm respectively). This trend is the same for the breadth.

##### Specimen 2103

This specimen falls entirely within the (fossil part of the) *C. l. familiaris* sample and population ranges and within the *C. l. lupus* sample ranges for both the length and breadth (table 4.34, fig. 4.30 and fig. VII.10). Specimen 2103 only partly overlaps with the lower part of the *C. l. lupus* population range for the length, the upper part of the *Cuon alpinus* sample and population ranges for the length and the upper part of the *Cuon alpinus* sample range for the breadth. 2103 Falls entirely outside (below) the *C. l. lupus* population range and (above) the *Cuon alpinus* population range for the breadth. The mean value of specimen 2103 for the length (22.40 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 1.15 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 1.91 mm) and most dissimilar to the average *C. l. lupus* specimen (with 4.79 mm) (appendix XIII). This trend is the same for the breadth.

##### Specimen 2104

In this fossil North Sea specimen the  $M_1$  is partly eroded on the labial side of the tooth, as a result of which the breadth of the tooth could not be measured (appendix I). Specimen 2104 falls entirely within the *Cuon alpinus* and *C. l. familiaris* (fossil part) sample and population ranges, partly outside (below) the *C. l. lupus* sample range and entirely outside (below) the *C. l. lupus* population range for the length of  $M_1$  (table 4.34, fig. 4.30 and fig. VII.10). The mean value of specimen 2104 for the length (21.32 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.07 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 0.83 mm) and most dissimilar to the average *C. l. lupus* specimen (with 5.87 mm) (appendix XIII).

##### Specimen 2196

The specimen range of 2196 falls entirely outside (far above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* and within the *C. l. lupus* sample and population ranges (table 4.34 and fig. 4.30). The mean value of specimen 2196 for the length (30.19 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 3.00 mm between the two mean values) and much more dissimilar to the

average *C. l. familiaris* and *Cuon alpinus* specimens (with 8.94 and 9.70 mm respectively), which is also very obvious from fig. 4.30 in which 2196 plots in the upper part. This trend is the same for the breadth.

#### **Specimen 2329**

Specimen 2329 falls entirely outside (above) the sample and population ranges of *C. l. familiaris* for the length and entirely outside (above) the sample and population ranges of *Cuon alpinus* for both the length and breadth of  $M_1$  (table 4.34 and fig. 4.30). The specimen range slightly overlaps with the upper part of the *C. l. familiaris* sample and population ranges for the breadth and falls entirely within the *C. l. lupus* sample and population ranges for the length and breadth. The mean value of specimen 2329 for the length (28.87 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 1.68 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 7.62 and 8.38 mm respectively) (appendix XIII). This trend is the same for the breadth. From fig. 4.30 can be seen that also this specimen has a quite small  $M_1$  compared to the length of this molar.

#### **Specimen 2620**

Specimen 2620 falls entirely outside (far above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* and within the *C. l. lupus* sample and population ranges (table 4.34 and fig. 4.30). The mean value of specimen 2620 for the length (30.22 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 3.03 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 8.97 and 9.73 mm respectively), which is also obvious from fig. 4.30. This trend is the same for the breadth.

#### **Specimen 3219**

The specimen range of this specimen falls entirely within the (fossil part of the) *C. l. familiaris* sample and population ranges and the *C. l. lupus* sample ranges for both the length and breadth of  $M_1$  (table 4.34, fig. 4.30 and fig. VII.10). Specimen 3219 falls partly below the *C. l. lupus* population range for the length, partly above the *Cuon alpinus* sample and population ranges for the length and partly above the *Cuon alpinus* sample range for the breadth. This specimen falls entirely outside (above) the *Cuon alpinus* population range and entirely outside (below) the *C. l. lupus* population range for the breadth. The mean value of specimen 3219 for the length (22.80 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 1.55 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 2.31 mm) and most dissimilar to the average *C. l. lupus* specimen (with 4.39 mm) (appendix XIII). This trend is the same for the breadth.

#### **Specimen 3293**

Specimen 3293 falls entirely outside (above) the *C. l. familiaris* and *Cuon alpinus* sample and population ranges and within the *C. l. lupus* sample and population ranges (table 4.34). The mean value of specimen 3293 for the length (27.12 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.07 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 5.87 and 6.63 mm respectively), which is also obvious from fig. 4.30. This trend is the same for the breadth.

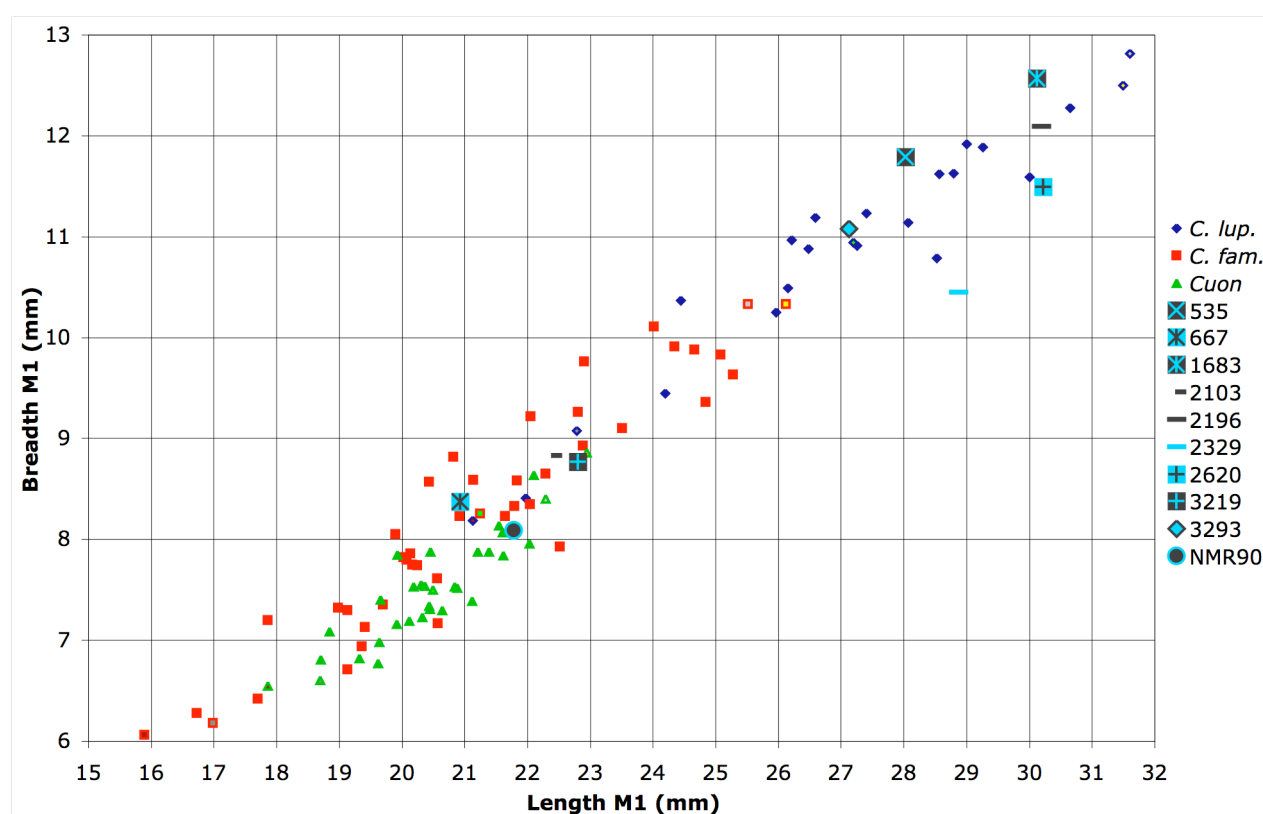
#### **Specimen NMR90**

NMR90 falls entirely within the (fossil part of the) *C. l. familiaris* sample and population ranges for the length and breadth, within the *Cuon alpinus* sample range for length and within the *Cuon alpinus* sample and population ranges for the breadth (table 4.34, fig. 4.30 and fig. VII.10). NMR90 partly falls outside (below) the *C. l. lupus* sample ranges for the length and breadth and partly outside (above) the *Cuon alpinus* population range for the length. Finally, this specimen falls entirely outside the *C. l. lupus* population ranges for both the length and breadth of  $M_1$ . The mean value of specimen NMR90 for the length (21.78 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.53 mm between the two mean values), less similar to the average *Cuon alpinus* specimen (with 1.29 mm) and most dissimilar to the average *C. l. lupus* specimen (with 5.41 mm) (appendix XIII). This trend is the same for the breadth.



**Table 4.34: Comparison of the specimen ranges of the fossil North Sea specimens with the sample and population ranges of the comparative material for parameters 'Length' (left) and 'Breadth' (right) of  $M_1$  (in mm).** Sample and population ranges of the comparative material are as given in table 4.33. Specimen ranges were calculated as explained in table 4.2.

Canidae material		Length $M_1$				Breadth $M_1$			
		- Sample range +		- Population range +		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	21,13	31,49	22,79	31,60	8,19	12,5	9,08	12,8
	<i>C. l. familiaris</i>	15,89	26,12	16,98	25,52	6,06	10,3	6,18	10,3
	<i>Cuon alpinus</i>	17,86	22,94	18,69	22,28	6,55	8,86	6,61	8,40
Fossil North Sea	535	27,19	28,87	-	-	11,57	12,01	-	-
	667	20,09	21,77	-	-	8,15	8,59	-	-
	1683	29,28	30,96	-	-	12,35	12,79	-	-
	2103	21,56	23,24	-	-	8,61	9,05	-	-
	2104	20,48	22,16	-	-	-	-	-	-
	2196	29,35	31,03	-	-	11,87	12,31	-	-
	2329	28,03	29,71	-	-	10,23	10,67	-	-
	2620	29,38	31,06	-	-	11,27	11,71	-	-
	3219	21,96	23,64	-	-	8,55	8,99	-	-
	3293	26,28	27,96	-	-	10,86	11,30	-	-
	NMR90	20,94	22,62	-	-	7,87	8,31	-	-



**Figure 4.30: Scatter plot of parameters 'Length' vs. 'Breadth' of  $M_1$  for the fossil North Sea specimens and the comparative material (in mm).** Legend, see tables 4.1 and 4.2.

#### Values from literature

For the length and breadth of  $M_1$  values of comparative *Cuon alpinus* specimens were found in literature (Adam (1959) and Pérez Ripoll et al (2010)) that fall outside (above) the sample and/or population ranges that were already calculated based on the original comparative dataset (table IX.5). For the length of  $M_1$  values of 28 *Cuon alpinus* specimens and for the breadth of  $M_1$  values of 23 *Cuon alpinus* specimens were added to the comparative dataset (which resulted in a sample size of respectively 55 and 50 instead of 27). New statistics were calculated and the fossil North Sea specimens were compared to the new ranges (table IX.6 and appendix XII).

Following results concern the length of  $M_1$

For specimens 535, 667, 1683, 2104, 2196, 2329, 2620 and 3293 the results obtained by the comparison to the new comparative ranges confirm previous results: specimens 667 and 2104 still fall entirely within both the *Cuon alpinus* sample and population ranges and all other specimens still fall entirely outside the *Cuon alpinus* sample and population ranges (appendix XII). Specimens 2103 and 3219 originally fell partly outside both *Cuon alpinus* ranges, but fall entirely within both new ranges. Specimen NMR90 originally fell within the *Cuon alpinus* sample range and partly outside corresponding population range, but falls entirely within both new ranges.

Following results concern the breadth of  $M_1$

For the following specimens the results obtained by the comparison to the new comparative ranges confirm previous results: specimen NMR90 still falls entirely within the *Cuon alpinus* sample and population ranges and specimens 535, 1683, 2196, 2620 and 3293 still fall entirely outside both *Cuon alpinus* ranges (appendix XII). Specimen 667 originally fell within the *Cuon alpinus* sample range and partly outside the population range, but falls entirely within both new *Cuon alpinus* ranges. Specimens 2103 and 3219 fell originally partly outside the *Cuon alpinus* sample range and entirely outside corresponding population range, but fall entirely within both *Cuon alpinus* ranges for the new extended dataset. Specimen 2329 originally fell outside the *Cuon alpinus* sample and population ranges, but falls only partly outside the new *Cuon alpinus* population range.

#### 4.4.3.2 Length and breadth of $M_2$

##### 4.4.3.2a Results comparative material

For all values mentioned below see both table 4.35 and fig. 4.31 unless stated otherwise.

**x** With 11.4 mm *C. l. lupus* has on average the biggest length for  $M_2$ , followed by *C. l. familiaris* (9.09 mm) and *Cuon alpinus* (7.04 mm). Values are smaller for the breadth of  $M_2$  but the trend is the same: *C. l. lupus* has clearly the widest molars and the average values for *Cuon alpinus* and *C. l. familiaris* are lower and lie closer together (table 4.35).

**SD vs. n** For both the length and breadth of  $M_2$  *C. l. familiaris* has the greatest sample size (36) and also the largest variation, but the standard deviation of *C. l. lupus* lies very close to the value of *C. l. familiaris*, while the sample size of this species is much smaller (17). *Cuon alpinus* is again the species with the lowest variation, while its sample size is quite large (table 4.35).

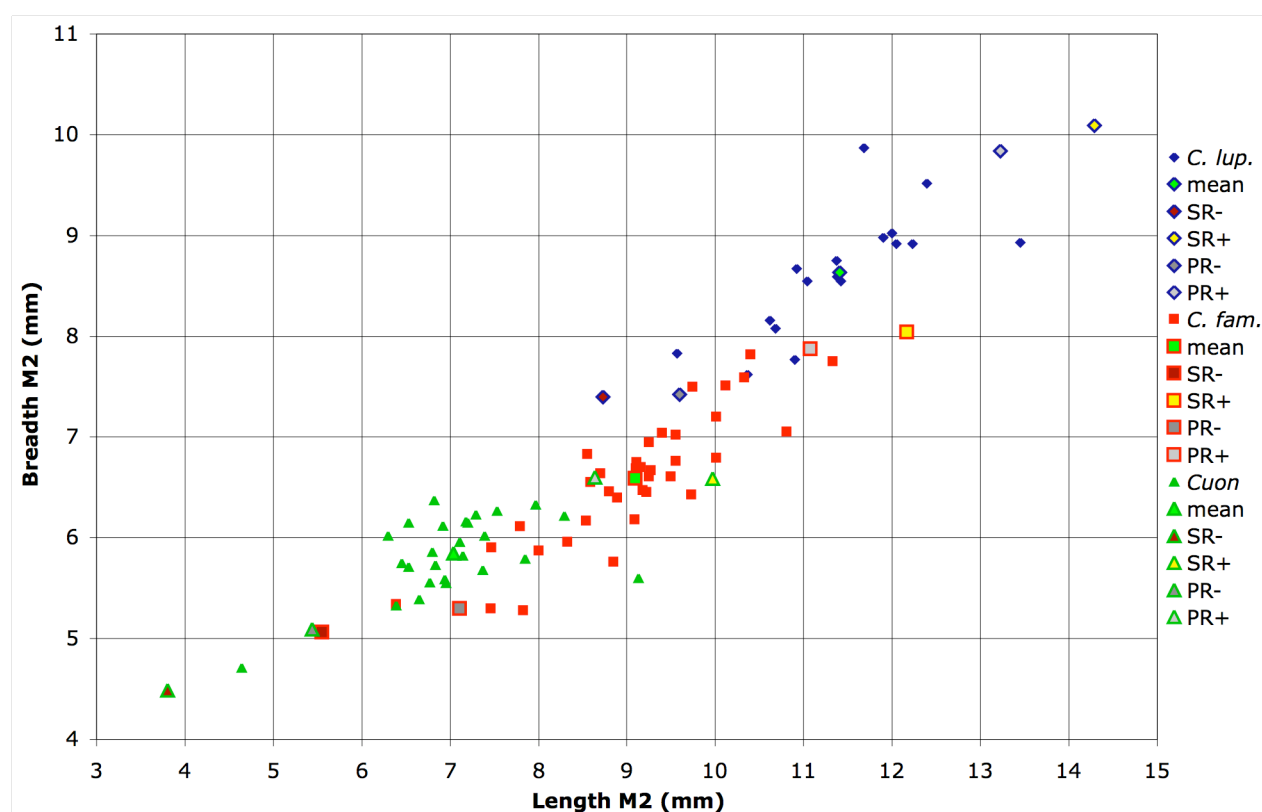
**Sample ranges:** see table 4.35. For the length the *Cuon alpinus* and *C. l. lupus* ranges slightly overlap (with 1.24 mm), but not for breadth, which can be seen in fig. 4.31: the *Cuon alpinus* and *C. l. lupus* data clouds are nicely separated. *C. l. familiaris* specimens plot mainly in between the mean values of these two species. The distinction in the *C. l. familiaris* group, separating the fossil specimens from the Netherlands from the recent specimens from Suriname is the same as for previous parameters: recent specimens plot over the entire *C. l. familiaris* range, while the fossil specimens are concentrated in the upper part of the *C. l. familiaris* range (fig. VII.11). For this parameter the data points of both *Canis* species plot evenly over their ranges in a quite linear way; there are no remarkable specimens that have an extremely low or high value for the breadth of  $M_2$  in proportion to the length (fig. 4.31). *Cuon alpinus* specimens plot more in a circular data cloud than both *Canis* species, of which the data clouds are more elongated. One *Cuon alpinus* specimen (20551) has a quite short and small  $M_2$  compared to the other *Cuon alpinus* specimens.

**Population ranges:** see table 4.35. The population ranges of *Cuon alpinus* and *C. l. lupus* do not overlap for both the length and breadth of  $M_2$ , but *C. l. familiaris* still overlaps greatly with these both species.

**Trend lines** All three comparative species have slightly more variation in the length of  $M_2$  than in the breadth, but in general the two parameters are quite similar and data points plot on a nice linear line: the length and breadth of  $M_1$  are well comparable (fig. 4.31). *Cuon alpinus* specimens plot in a more circular than linear data clouds, thus it would not make sense to plot a trend line for this species. When plotted, the trend lines of *C. l. familiaris* and *C. l. lupus* show an offset with respect to each other, but the position of the fossil North Sea specimens is already clear without these trend lines. Trend lines would thus not be an aid in the identification of the fossil North Sea specimens and are not discussed.

**Table 4.35: Statistics of the parameters 'Length' (left) and 'Breadth' (right) of  $M_2$  of the comparative material (in mm).** Legend: see table 4.1.

Statistics	Length $M_2$			Breadth $M_2$		
	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>
Sample size (n)	17	36	26	17	36	26
Sample mean ( $\bar{x}$ )	11,4	9,09	7,04	8,63	6,59	5,85
Standard deviation (SD)	0,91	0,99	0,80	0,60	0,64	0,38
Minimum (MIN)	9,57	6,39	4,64	7,62	5,28	4,71
Maximum (MAX)	13,5	11,3	9,13	9,87	7,82	6,37
Sample range MIN	8,73	5,55	3,80	7,40	5,06	4,49
Sample range MAX	14,3	12,2	9,97	10,1	8,04	6,59
Population range MIN	9,60	7,11	5,43	7,43	5,30	5,10
Population range MAX	13,2	11,1	8,64	9,84	7,87	6,60



**Figure 4.31: Scatter plot of parameters 'Length' vs. 'Breadth' of  $M_2$  for the comparative material (in mm).** Legend, see table 4.1.

#### 4.4.3.2b Results fossil North Sea material

Not all 13 fossil North Sea specimens had values for both parameters, thus only 8 specimens could be plotted in fig. 4.32.

##### Specimens 534 and 535

Results for these two specimens are exactly the same. Both specimens fall entirely within the sample and population ranges of *C. l. lupus* for both the length and breadth of  $M_2$  (table 4.36 and fig. 4.32). Specimens 534 and 535 fall entirely outside (above) the *C. l. familiaris* population ranges and *Cuon alpinus* sample and population ranges for the length and breadth. Both specimens also fall entirely outside (above) the *C. l. familiaris* sample range for the breadth, but partially within the *C. l. familiaris* sample range for the length of  $M_2$ . The mean value of specimen 534 for the length (12.28 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.87 mm between the two mean values) and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 3.19 and 5.24 mm respectively), which is also obvious from fig. 4.32. Values are very similar for specimen 535 and this trend is the same for the breadth for both specimens.

### **Specimen 667**

Specimen 667 falls entirely within the (fossil part of the) *C. l. familiaris* sample and population ranges for the length and breadth of  $M_2$  and within the *Cuon alpinus* sample and population ranges for the breadth (table 4.36, fig. 4.32 and fig. VII.11). 667 partly falls outside (below) the *C. l. lupus* population range for the length, but within corresponding sample range and partly above the *Cuon alpinus* sample range for the length. This specimen falls entirely outside (below) the *C. l. lupus* sample and population ranges for the breadth and entirely above the *Cuon alpinus* population range for the length of the tooth. The mean value of specimen 667 for the length (9.58 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.49 mm between the two mean values), less similar to the average *C. l. lupus* specimen (with 1.83 mm) and most dissimilar to the average *Cuon alpinus* specimen (with 2.54 mm) (appendix XIII). This trend is partly reversed for the breadth of  $M_2$ : for this parameter 667 also is most similar to the average *C. l. familiaris* specimen, but more similar to the average *Cuon alpinus* than *C. l. lupus* specimen.

### **Specimen 1683**

Specimen 1683 falls entirely within the *C. l. lupus* sample and population ranges and entirely outside (above) the *Cuon alpinus* sample and population ranges for both the length and breadth of  $M_2$  (table 4.36 and fig. 4.32). This specimen also falls entirely outside (above) the *C. l. familiaris* sample and population ranges for the breadth, but still partly overlaps with the upper part of both the sample and population range for the length. The mean value of specimen 1683 for the length (11.80 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.39 mm between the two mean values) and less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 2.71 and 4.76 mm respectively), which is also obvious from fig. 4.32. This trend is the same for the breadth.

### **Specimens 2103, 2329, 3219, NMR89 and NMR90**

These five fossil North Sea specimens miss an  $M_2$  (plate 4.1) thus the length and breadth could not be measured.

### **Specimen 2104**

This fossil North Sea specimen falls entirely within the (fossil part of the) *C. l. familiaris* sample and population ranges for both the length and breadth of  $M_2$  and entirely outside (below) the *C. l. lupus* sample and population ranges for the breadth (table 4.36, fig. 4.32 and fig. VII.11). 2104 Partly falls outside (below) the *C. l. lupus* sample and population ranges for the length and partly above the *Cuon alpinus* sample and population ranges for both the length and breadth. The mean value of specimen 2104 for the length (9.35 mm) is most similar to the average *C. l. familiaris* specimen (with a distance of 0.26 mm between the two mean values), less similar to the average *C. l. lupus* specimen (with 2.06 mm) and most dissimilar to the average *Cuon alpinus* specimen (with 2.31 mm) (appendix XIII). This trend is partly reversed for the breadth of  $M_2$ ; for this parameter 2104 also is most similar to the average *C. l. familiaris* specimen, but more similar to the average *Cuon alpinus* than *C. l. lupus* specimen.

### **Specimen 2196**

This specimen falls entirely outside (above) the *Cuon alpinus* sample and population ranges for both the length and breadth of  $M_2$  and entirely outside (above) the *C. l. familiaris* sample and population ranges for the breadth (table 4.36 and fig. 4.32). Specimen 2196 partly overlaps with the upper part of the *C. l. familiaris* sample range for the length and falls entirely outside (above) corresponding population range. 2196 Falls entirely within the *C. l. lupus* sample and population ranges for the breadth, within the *C. l. lupus* sample range for the length and partly outside (above) corresponding population range. The mean value of specimen 2196 for the length (12.51 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 1.10 mm between the two mean values) and much less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 3.42 and 5.47 mm respectively), which is also obvious from fig. 4.32. This trend is the same for the breadth (for which 2196 is very similar to the average *C. l. lupus* specimen, with only a distance of 0.01 mm between the two mean values).

### **Specimen 2620**

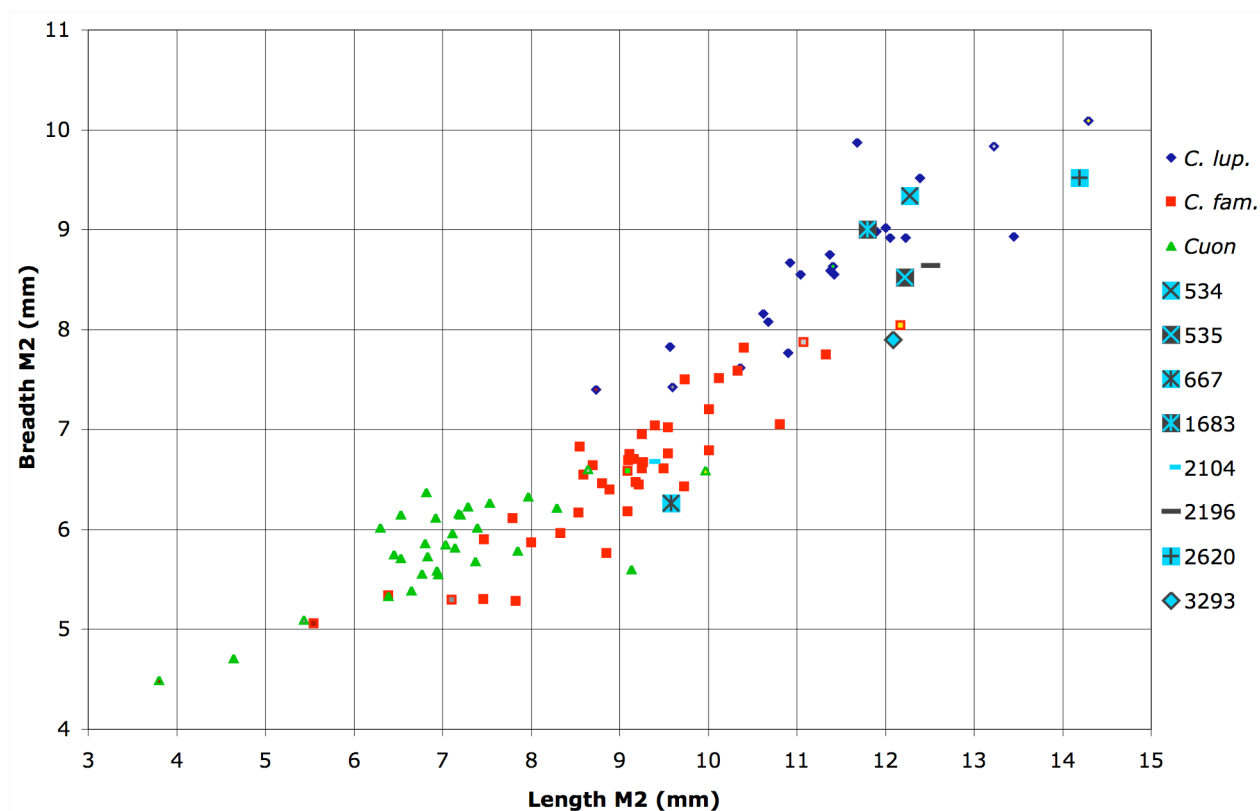
Specimen 2620 falls entirely outside (far above) the *C. l. familiaris* and *Cuon alpinus* sample and population ranges for both the length and breadth of  $M_2$  (table 4.36 and fig. 4.32). This specimen falls entirely within the *C. l. lupus* sample and population ranges for the breadth, but has such a large second molar that the specimen range partly falls outside (above) the sample range and entirely above the population range for the length. The mean value of specimen 2620 for the length (14.19 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 2.78 mm between the two mean values) and much less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 5.10 and 7.15 mm respectively), which is also obvious from the position of 2620 in the upper part of fig. 4.32. This trend is the same for the breadth.

### Specimen 3293

Specimen 3293 falls entirely outside the *Cuon alpinus* sample and population ranges for both the length and breadth and entirely outside (above) the *C. l. familiaris* population range for the length (table 4.36 and fig. 4.32). This specimen falls partly outside (above) the sample and population ranges of *C. l. familiaris* for the breadth of  $M_2$ , partially above the sample range of *C. l. familiaris* for the length and entirely within all *C. l. lupus* ranges. The mean value of specimen 3293 for the length (12.09 mm) is most similar to the average *C. l. lupus* specimen (with a distance of 0.68 mm between the two mean values) and much less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens (with 3.00 and 5.05 mm respectively) (appendix XIII and fig. 4.32). This trend is the same for the breadth.

**Table 4.36: Comparison of the specimen ranges of the fossil North Sea specimens with the sample and population ranges of the comparative material for parameters 'Length' (left) and 'Breadth' (right) of  $M_2$  (in mm).** Sample and population ranges of the comparative material are as given in table 4.35. Specimen ranges were calculated as explained in table 4.2.

Canidae material		Parameter x				Parameter x			
		- Sample range +		- Population range +		- Sample range +		- Population range +	
Comp.	<i>C. l. lupus</i>	8,73	14,3	9,60	13,2	7,40	10,1	7,43	9,84
	<i>C. l. familiaris</i>	5,55	12,2	7,11	11,1	5,06	8,04	5,30	7,87
	<i>Cuon alpinus</i>	3,80	9,97	5,43	8,64	4,49	6,59	5,10	6,60
Fossil North Sea	534	11,44	13,12	-	-	9,12	9,56	-	-
	535	11,38	13,06	-	-	8,30	8,74	-	-
	667	8,74	10,42	-	-	6,04	6,48	-	-
	1683	10,96	12,64	-	-	8,78	9,22	-	-
	2104	8,51	10,19	-	-	6,46	6,90	-	-
	2196	11,67	13,35	-	-	8,42	8,86	-	-
	2620	13,35	15,03	-	-	9,30	9,74	-	-
	3293	11,25	12,93	-	-	7,68	8,12	-	-



**Figure 4.32: Scatter plot of parameters 'Length' vs. 'Breadth' of  $M_2$  for the fossil North Sea specimens and the comparative material (in mm).** Legend, see tables 4.1 and 4.2.

### Values from literature

The breadth of  $M_2$  is the last parameter for which values of comparative *Cuon alpinus* specimens were found in literature (Adam (1959) and Pérez Ripoll et al (2010)). For this parameter values of 16 *Cuon alpinus* specimens were added to the comparative dataset (which resulted in a sample size of 42 instead of 26) (table IX.5). New statistics were calculated and the fossil North Sea specimens were compared to the new ranges (table IX.6 and appendix XII).

For specimens 534, 535, 667, 1683, 2196, 2620 and 3293 the results obtained by the comparison to the new comparative ranges confirm previous results: specimen 667 still falls entirely within the *Cuon alpinus* sample and population ranges and specimens 534, 535, 1683, 2196, 2620 and 3293 still fall entirely outside both *Cuon alpinus* ranges (appendix XII). Results for specimen 2104 were different: the specimen range of 2104 originally fell partially outside both *Cuon alpinus* ranges, but falls entirely within the new *Cuon alpinus* sample and population ranges.

### 4.4.4 Cusps on premolars

The presence, amount and appearance of the different cusps that can be present in *Canis* and *Cuon alpinus* premolars (box III.3 and IV.4) was recorded to investigate whether there are important differences between the two *Canis* species and *Cuon alpinus* that can be used to identify the fossil North Sea specimens. The sample sizes of the comparative species can be smaller than in previous parameters, because in many specimens teeth are eroded or missing as a result of which no information could be obtained for the cusps (plate 4.1). The  $P_1$  is a small and round tooth with only one principal cusp (protoconid) in both *Canis* and *Cuon alpinus*. There is a difference in appearance of this cusp in the two genera, but this was already briefly discussed earlier in this section (4.4.2.1). In this paragraph only results of  $P_2$ - $P_4$  will be discussed.

#### **Results comparative and fossil North Sea material**

For all results concerning the cusps on premolars of all individual fossil North Sea and comparative specimens, see appendix XIII. The presence and amount of accessory cusps and other mesial and distal tooth structures are highly variable within species. In the premolars of all three comparative species tooth structures are often not present mesially of the protoconid or not distinctly present (a cingulum is present, but no clear parastylid) (table 4.37). Of the fossil North Sea specimens only specimen 2620 has a mesial structure: a cingulum (appendix XIII). A general trend can be seen in all three comparative species of an increase in the occurrence of the parastylid from  $P_2$  to  $P_4$ , because the length of the tooth increases from  $P_2$  to  $P_4$ ; there is thus more space for accessory cusps (table 4.37). Especially in *Cuon alpinus* a parastylid is present on the  $P_4$  in many specimens (74%) on the contrary to *Canis*, but it could very well be that this apparent difference is an effect of this particular dataset, because the presence and amount of mesial tooth structures is highly variable. Based on this difference no conclusions can be drawn about the identity of the fossil North Sea specimens.

A protoconid (the principal cusp of the premolars) is always present in all comparative species and a metastylid is also present in all  $P_3$  and  $P_4$  of both *Canis* species and *Cuon alpinus* (table 4.37). A metastylid is also present in most *Canis* specimen in the  $P_2$  and in a significant amount of the *Cuon alpinus* specimens. There are neither major differences for these tooth structures between *Canis* and *Cuon alpinus*, although again the trend is observed of an increase in accessory cusps from  $P_2$  to  $P_4$ . Almost all fossil North Sea specimens for which cusps of premolars could be analyzed (667 – 3293) also possessed a protoconid and metastylid on their  $P_2$ ,  $P_3$  and  $P_4$  (appendix XIII).

Distal tooth structures were only recorded for  $P_3$  and  $P_4$ , because they very rarely occur in all three species. Many *Canis* specimens possess a metaconulid on both their  $P_3$  and  $P_4$ , while in *Cuon alpinus* a metaconulid is not frequently present on the  $P_3$ , but always on the  $P_4$  (table 4.37). Also the occurrence of distal cusps increases from  $P_3$  to  $P_4$ . Although the occurrence of a metaconulid in *Cuon alpinus* does not entirely resemble the trend observed in *Canis*, the observed differences are not sufficiently solid to base conclusions on. All fossil North Sea specimens for which cusps of  $P_3$  and  $P_4$  could be analyzed (667 – NMR90) possessed a cingulum on their  $P_3$  and a metaconulid on their  $P_4$  (except specimen 2196 which had a metaconulid on its  $P_3$  and specimen 3219 which had a cingulum on its  $P_4$ , appendix XIII).

There are no major differences in the presence, amount and appearance of the different cusps that can be present in *Canis* and *Cuon* premolars. The cusps of the premolars can thus not be used to identify the fossil North Sea specimens and will not be discussed any further.

**Table 4.37: Presence of dental topographical features on the P<sub>2</sub>, P<sub>3</sub> and P<sub>4</sub> of the comparative material (in %).** Percentages indicate in how much percent of the specimens the dental structure was distinctly present. Not included are specimens in which the dental structure was present, but only cingular. The average sample size for the comparative (sub)species was: *C. l. lupus* (16), *C. l. familiaris* (34), *Cuon alpinus* (26). For an explanation of the dental structures, see: box III.3.

Presence of dental topographical features on premolars of the Canidae material (%)			
Dental feature	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>
P <sub>2</sub> mesial	6	9	0
P <sub>2</sub> protoconid	100	100	100
P <sub>2</sub> metastyliid	81	74	31
P <sub>3</sub> mesial	13	3	0
P <sub>3</sub> protoconid	100	100	100
P <sub>3</sub> metastyliid	100	100	100
P <sub>3</sub> distal	56	56	12
P <sub>4</sub> mesial	13	22	74
P <sub>4</sub> protoconid	100	100	100
P <sub>4</sub> metastyliid	100	100	100
P <sub>4</sub> distal	94	89	100

## 4.4.5 Cusps on molars

The presence, amount and appearance of the principal cusps that can be present in *Canis* and *Cuon alpinus* molars was recorded to investigate whether there are significant differences between the two *Canis* species and *Cuon alpinus* that can be used to identify the fossil North Sea specimens.

### 4.4.5.1 Cusps of M<sub>1</sub>

#### 4.4.5.1a Results comparative material

For all percentages mentioned below see table 4.38 and for all individual values of the comparative specimens see appendix XIII. In all *Canis* specimens the M<sub>1</sub> is developed as carnassial tooth (Thenius, 1989) and a high trigonid including the protoconid, paraconid and metaconid and a shorter and smaller talonid including the hypoconid (buccal) and entoconid (lingual) is present. All five principal cusps are present as a pronounced and well individualized cusp and confirm the assignment to the genus *Canis* (García and Arsuaga, 1998) (table 4.38). The M<sub>1</sub> is also developed as carnassial tooth in *Cuon alpinus* (Thenius, 1989) and in all *Cuon alpinus* specimens the protoconid, paraconid and hypoconid are always present as a pronounced and well individualized cusp, as was the case in *Canis*. But where the metaconid and entoconid were always present in *Canis* they are absent in most *Cuon alpinus* specimens. In *Cuon alpinus* the metaconid was reduced in time (Thenius, 1989), on the contrary to *Canis*, but a few *Cuon alpinus* specimens still possess this cusp. In most *Cuon alpinus* specimens (67%) a metaconid is entirely absent in the trigonid, in 19% (5 specimens) a well individualized metaconid is present and in 15% (4 specimens) only a weak metaconid is present (table 4.38). This weak metaconid is much less individualized than the typical *Canis* metaconid and can clearly be distinguished from a *Canis* metaconid, but the well individualized metaconid of the five *Cuon alpinus* specimens is identical to a *Canis* metaconid. All *Cuon alpinus* specimens that possess this well individualized metaconid also have an entoconid. The entoconid is also absent in most *Cuon alpinus* specimens (85%) and in this case the conical hypoconid is centered in the talonid, whereas the hypoconid is buccal in *Canis*. The talonid is thus single cusped in *Cuon alpinus* “...while all other canids within the range of *Cuon* have two cusps. Single crested cusps on lower carnassial M<sub>1</sub> may enhance the shearing capacity of the teeth and hence the speed at which prey can be consumed. This may improve the dholes’ ability to compete with kleptoparasites.” (Durbin et al., 2008). The centered position of the hypoconid and the often-missing entoconid are usual features of *Cuon alpinus* (Pérez Ripoll et al., 2010). In 15% (4) of the *Cuon alpinus* specimens a small cingulum-like tooth structure is present between the hypoconid and the lingual edge of the M<sub>1</sub> that looks like a small entoconid (table 4.38). However, this *Cuon alpinus* entoconid is cingulum-like, not well individualized and does not result in a talonid basin as a *Canis* entoconid. This entoconid can thus clearly be distinguished from typical *Canis* entoconids. These four *Cuon alpinus* specimens in which an entoconid was present also possessed a metaconid. Due to the mostly missing meta- and entoconid, *Cuon alpinus* specimens have a small M<sub>1</sub> in which the three principal cusps (proto-, para- and hypoconid) are aligned and centered. *Canis* specimens on the other hand have five principal cusps, which are more positioned on the lingual and buccal sides of the M<sub>1</sub> as a result of which the tooth is broader.

Due to the two extra cusps in *Canis*, the two *Canis* subspecies also have a clear talonid and trigonid basin in their M<sub>1</sub>, where this is absent in *Cuon alpinus*, because of the centered cusps.

**Table 4.38: Presence of the principal cusps on the M<sub>1</sub> of the comparative material (in %).** Percentages in the first three columns indicate in how much percent of the specimens the cusp was present, including the specimens in which the cusp had an appearance that is different from the typical cusp. The second *Cuon alpinus*\* column indicates in how much percent of the specimens the cusp was present, only including the specimens in which, based on the appearance of the cusp, one cannot conclude whether the specimen is *Cuon alpinus* or *Canis*. The average sample size for the comparative (sub)species was: *C. l. lupus* (18), *C. l. familiaris* (38), *Cuon alpinus* (27). For an explanation of the dental topography, see: box III.3.

Presence of principal cusps on the M <sub>1</sub> of the Canidae material (%)				
Cusp	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>Cuon alpinus</i> *
M <sub>1</sub> paraconid	100	100	100	100
M <sub>1</sub> protoconid	100	100	100	100
M <sub>1</sub> metaconid	100	100	33	19
M <sub>1</sub> hypoconid	100	100	100	100
M <sub>1</sub> entoconid	100	100	15	0

#### 4.4.5.1b Results fossil North Sea material

For all results mentioned below see plate 4.2 and appendix XIII.

##### Specimens 534 and NMR89

These two fossil North Sea specimens miss an M<sub>1</sub> (plate 4.1) thus the presence, amount and appearance of the principal cusps could not be established.

##### Specimens 535, 1683 and 2103

These three fossil North Sea specimens have a high trigonid including a pronounced and well individualized protoconid, paraconid and metaconid and a shorter and smaller talonid including a pronounced and well individualized hypoconid (buccal) and entoconid (lingual). All five principal cusps are present in the broad M<sub>1</sub>.

##### Specimens 667, 2104, 2196, 2329, 2620, 3219 and 3293

In these seven fossil North Sea specimens one or more cusps are eroded, but it could still be determined that these M<sub>1</sub> clearly have a high trigonid including a pronounced and well individualized protoconid, paraconid and metaconid and a shorter and smaller talonid including a pronounced and well individualized hypoconid (buccal) and entoconid (lingual). All five principal cusps are present in the molars of these specimens (plate 4.2 and appendix XIII):

In specimen 667 the top of the para-, proto-, hypo- and entoconid are eroded off, but erosion was not severe and the five principal cusps could be easily identified in this broad M<sub>1</sub>. It could also be clearly determined that all cusps originally were well individualized.

In specimen 2104 the top of the para- and hypoconid are eroded and a large part of the protoconid and the entire metaconid are missing due to erosion, but a clear talonid basin is present. Although the original presence of a metaconid cannot be established with absolute certainty, this broad M<sub>1</sub> originally possessed at least a well individualized para-, proto-, hypo- and entoconid.

In specimen 2196 only part of the protoconid is eroded and the five well individualized principal cusps could be easily identified in this broad M<sub>1</sub>.

In specimen 2329 the top of the para-, proto-, hypo- and entoconid are eroded, but a clear talonid basin and metaconid are present. The five principal cusps could be easily identified in this broad M<sub>1</sub>.

The M<sub>1</sub> of specimen 2620 is severely eroded: a large mesial part of the tooth is missing, thus officially it cannot be established whether a proto-, para, and metaconid were originally present, but we can reasonably assume that a proto- and paraconid were at least present, since this is the case in all *Canis* and *Cuon alpinus* specimens. Although the original presence of a metaconid cannot be established with absolute certainty, this broad M<sub>1</sub> originally possessed at least a well individualized hypo- and entoconid and a talonid basin.

Specimen 3219 misses the top of its para-, proto- and hypoconid, but these conids including a metaconid are clearly present. A small distal part of the M<sub>1</sub> is eroded, but a clear talonid basin and half of the entoconid can clearly be identified in this broad distal part of the tooth.

Specimen 3293 is hardly eroded: only the top of the para-, proto-, and hypoconid are slightly eroded and the five well individualized principal cusps could be easily identified in this broad M<sub>1</sub>.



### Specimen NMR90

The  $M_1$  of NMR90 is highly eroded and only the para- and protoconid can be identified as well individualized cusps (plate 4.2). The meta-, hypo- and entoconid cannot be directly identified on this  $M_1$ , although some features are observed on this  $M_1$  that are related to these cusps. On the labial side of the protoconid, halfway up the tooth a tiny groove is visible that in *Canis* specimens is caused by the presence of a metaconid (see stippled line in fig. III.1 between the proto- and metaconid). The broad talonid is highly eroded and polished and no remains of a hypoconid or entoconid are visible, but a clear indentation is present between the distolingual part of the protoconid and the distolingual edge of the talonid (see stippled line in fig. III.1 between the meta- and entoconid). In *Cuon alpinus* specimens this indentation is never present, because the cusps are centered and surrounded by a continuous edge. Except for the broad talonid, there are no indications for the presence of a hypoconid, but it can reasonably be assumed that this cusp was present, because it was present in all comparative specimens.

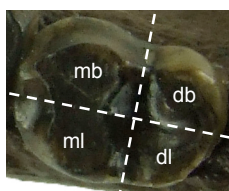
### 4.4.5.2 Cusps of $M_2$

#### 4.4.5.2a Results comparative material

For all percentages mentioned below see table 4.39 and for all individual values of the comparative specimens see appendix XIII. In both *Cuon alpinus* and *Canis* specimens the  $M_2$  is not developed as carnassial tooth and thus much smaller than the  $M_1$ . In all specimens of both *Canis* species the  $M_2$  can be divided into four quadrants (fig. 4.33). The trigonid is two-cusped and consists of a well individualized protoconid in the mesiobuccal quadrant and a well individualized metaconid in the mesiolingual quadrant. The talonid always consists of a well individualized hypoconid in the distobuccal quadrant and an entoconid-like structure and talonid basin in the distolingual quadrant. In both *Canis* species the entoconid-like structure is mostly present in cingular form (96% of the specimens) and rarely as well discernable, well individualized entoconid (6%, which is respectively 1 and 2 specimens for *C. l. lupus* and *C. l. familiaris*) (table 4.39).

In all comparative *Cuon alpinus* specimens the protoconid and hypoconid are always present, as in *Canis*, but the metaconid and entoconid are often absent, as was the case for the  $M_1$  (table 4.39 and appendix XIII). The cusps also have a different appearance than those of *Canis*. The protoconid is present in all *Cuon alpinus* specimens, but is centered in the middle of the trigonid in 85% of the *Cuon alpinus* specimens. In only 15% (4) of the *Cuon alpinus* specimens the protoconid is positioned in the mesiobuccal quadrant as in *Canis*. The metaconid is absent in most *Cuon alpinus* specimens (81%), but, if present, only well individualized in 15% of the *Cuon alpinus* specimens. The hypoconid is also present in all *Cuon alpinus* specimens, but flat and not well individualized in 92% of the specimens. In only 2 *Cuon alpinus* specimens the hypoconid is similar in appearance to the well discernable *Canis* hypoconids. Finally, the entoconid is absent in 92% of the *Cuon alpinus* specimens, but if present it is cingular as in *Canis*. If we now combine the results of the four *Cuon alpinus* cusps (table 4.40), we can see that of the four *Cuon alpinus* specimens that possessed a protoconid in the mesiobuccal quadrant as in *Canis*, only two specimens also have a well individualized metaconid, but meanwhile also a flat and not well developed hypoconid and no entoconid. There are thus no *Cuon alpinus* specimens in this comparative dataset in which all cusps of the  $M_2$  are identical to those of *Canis*.

**Figure 4.33:  $M_2$  of fossil North Sea specimen 667 indicating of the mesiobuccal (mb), mesiolingual (ml), distobuccal (db) and distolingual (dl) quadrant of a typical *Canis*  $M_2$ .**



**Table 4.39: Presence of the principal cusps on the M<sub>2</sub> of the comparative material (in %).** Percentages in the first three columns indicate in how much percent of the specimens the cusp was present, including the specimens in which the cusp had an appearance that is different from the typical cusp. The second *Cuon alpinus*\* column indicates in how much percent of the specimens the cusp was present, only including the specimens in which, based on the appearance of the cusp, one cannot conclude whether the specimen is *Cuon alpinus* or *Canis*. The average sample size for the comparative (sub)species was: *C. l. lupus* (18), *C. l. familiaris* (36), *Cuon alpinus alpinus* (26). For an explanation of the dental topography, see: box III.3.

Presence of principal cusps on the M <sub>2</sub> of the Canidae material (%)				
Cusp	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>Cuon alpinus</i> *
M <sub>2</sub> protoconid	100	100	100	15
M <sub>2</sub> metaconid	100	100	19	15
M <sub>2</sub> hypoconid	100	100	100	8
M <sub>2</sub> entoconid	100	100	8	8

**Table 4.40: Presence of the principal cusps on the M<sub>2</sub> of the four comparative *Cuon alpinus* specimens that look identical to *Canis* based on the protoconid of their M<sub>2</sub>.** ‘Yes’ means that the cusp was present in its typical appearance. ‘Flat’ means that the cusp was not well developed. – Means that the cusp was absent. For an explanation of the dental topography, see: box III.3.

Presence of principal cusps on the M <sub>2</sub> of 4 comparative <i>Cuon alpinus</i> specimens				
Cusp	<i>Cuon</i> -a-java	<i>Cuon</i> -e	<i>Cuon</i> -h	33841
M <sub>2</sub> protoconid	yes	yes	yes	yes
M <sub>2</sub> metaconid	yes	yes	-	-
M <sub>2</sub> hypoconid	flat	flat	flat	flat
M <sub>2</sub> entoconid	-	-	-	-

#### 4.4.5.2b Results fossil North Sea material

For all results mentioned below see plate 4.2 and appendix XIII.

##### Specimens 534, 535, 667, 1683, 2104, 2620 and 3293

The following seven fossil North Sea specimens all have an M<sub>2</sub> that is divided into four quadrants: a clearly discernable and well individualized proto-, meta- and hypoconid is situated in the mesiobuccal, mesiolingual and distobuccal quadrant respectively and a talonid basin with entoconid-like cingulum occupies the fourth (distolingual) quadrant (fig. 4.33).

In specimen 534 the top of the proto- and hypoconid are slightly eroded, but the three principal and well developed cusps are clearly discernable and positioned in a quadrant-like manner as described above. A clear talonid basin, surrounded by a cingulum (not an individualized entoconid), occupies the fourth quadrant (plate 4.2).

The top of the protoconid of specimen 535 is slightly eroded, but the three principal and well developed cusps can be easily identified. All cusps and the talonid basin with cingulum are positioned in a quadrant.

In specimen 667 the top of the well individualized proto-, meta- and hypoconid are highly eroded, but these cusps could still be easily identified. Due to the erosion the indentations between the cusps and the talonid basin are accentuated and the quadrant-like shape of the tooth is evident (plate 4.2).

In specimen 1683 the top of the proto-, meta- and hypoconid are also highly eroded, but it is clear that these three cusps originally were present and well developed. Also in this specimen the cusps are each positioned in a quadrant and a talonid basin with cingulum occupies the fourth (distolingual) quadrant.

The cusps of specimens 2104 and 3293 were not eroded and the M<sub>2</sub> looks exactly as described above.

All cusps of the M<sub>2</sub> of specimen 2620 were somewhat eroded, but as in all previous specimens the M<sub>2</sub> is broad and can be divided into four quadrants, which each were originally occupied by a well individualized cusp or the talonid basin (plate 4.2).

The M<sub>2</sub> of specimen 3293 was not severely eroded and all three principal cusps could be easily identified.

##### Specimen 2196

In specimen 2196 the M<sub>2</sub> is quite large and broad as in typical *Canis* specimens, but the well individualized protoconid is centered in the trigonid as in typical *Cuon alpinus* specimens. A well individualized hypoconid is present on the buccal side of the talonid and lingual of the hypoconid a small talonid-basin-like depression is seen, which is bordered by a cingulum (plate 4.2 and appendix XIII).

##### Specimens 2103, 2329, 3219, NMR89 and NMR90

These five fossil North Sea specimens miss their M<sub>2</sub> thus presence of the cusps could not be established.

**Plate 4.2: Molar(s) of fossil North Sea specimens 535, 667, 1683, 2103, 2104, 2196, 2329, 2620, 3219, 3293 and NMR90 with indication of the cusps that are present. Bold number is the specimen reg. no. Pa = paraconid; Pr = protoconid; Me = metaconid; Hy = hypoconid; En = entoconid; cg = cingulum (box III.3). Directions: m = mesial; d = distal; b = buccal; l = lingual (box III.2).**

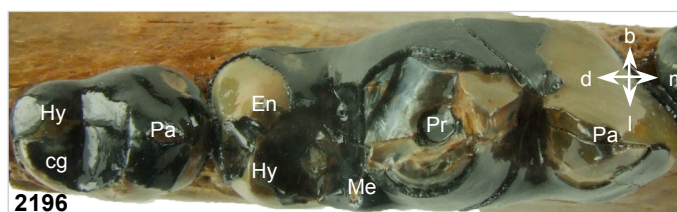
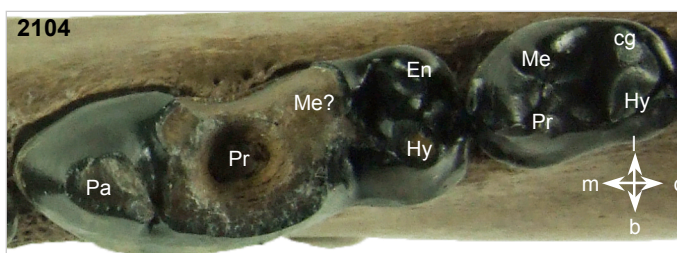
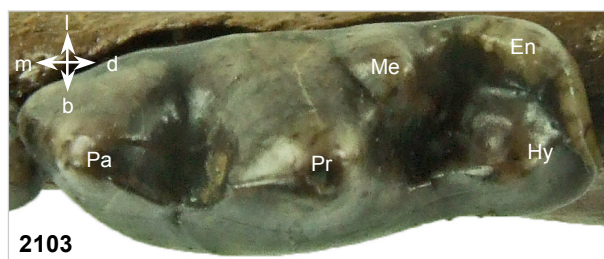
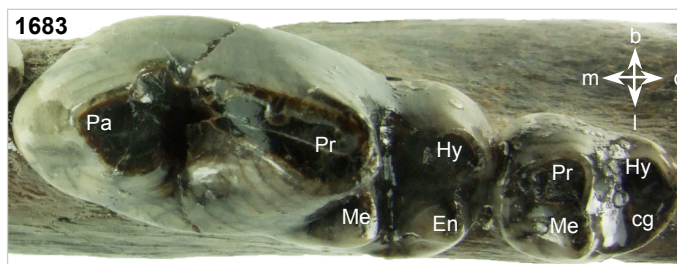
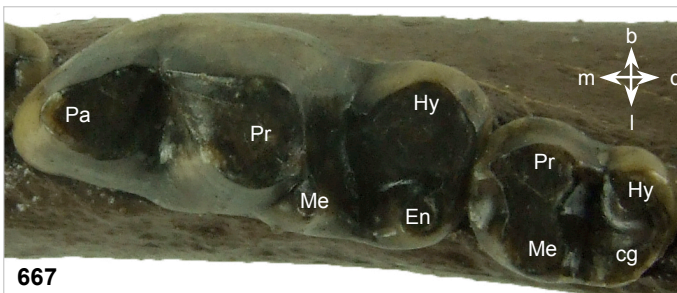
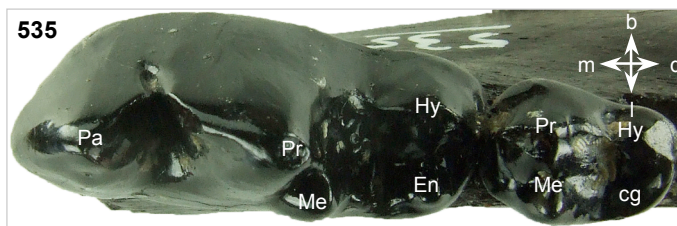
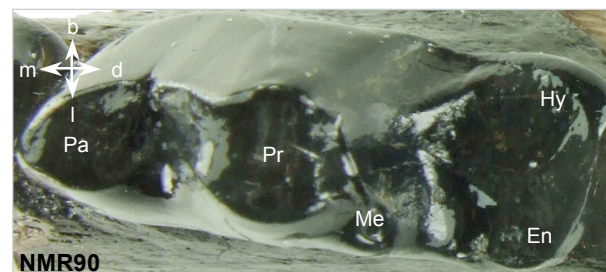
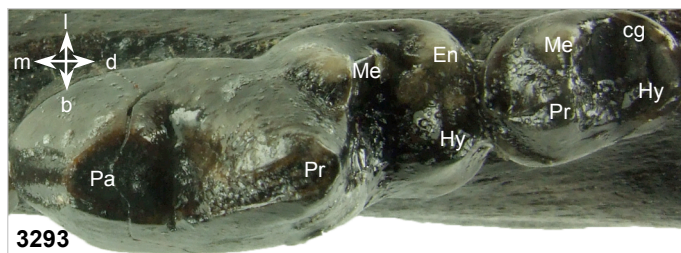
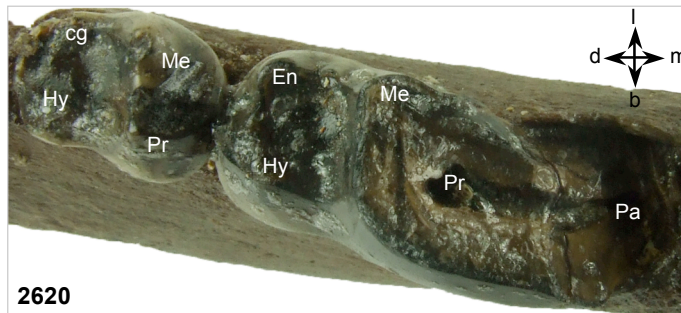
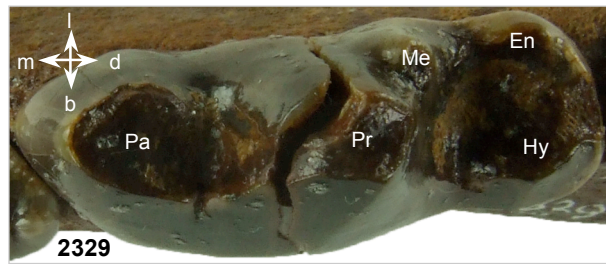


Plate 4.2 continued.



## 4.5 Summary of SD vs. n results

In the table below an overview is given of the results of the standard-deviation-versus-sample-size trend that was observed in all quantitative parameters. In paragraph 5.1.3 these results are briefly interpreted.

**Table 4.41: Summary of the standard deviation (SD) vs. the sample size (n) trend of *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* for each quantitative subparameter.** For each subparameter is given which of the three comparative (sub)species had the largest (++) , second largest (+) or smallest (-) SD. From left to right the comparative (sub)species have a decreasing sample size. Average sample sizes for all parameters are: *C. l. familiaris* (42); *Cuon alpinus* (27); *C. l. lupus* (18). +\* Indicates that the SD values of both *Canis* subspecies lie very close together, which means that, although the absolute SD of *C. l. lupus* is larger, the SD of *C. l. familiaris* is relatively larger in proportion to its sample size than the SD of *C. l. lupus*. For the abbreviations of the parameters: see appendix IV.

Parameter		Relative standard deviation		
		<i>C. l. familiaris</i>	<i>Cuon alpinus</i>	<i>C. l. lupus</i>
Mandible length	<i>a-b</i>	++	-	+
	<i>c-b</i>	++	-	+
Alveolar length	P <sub>1</sub> -M <sub>2</sub>	++	-	+*
	P <sub>4</sub> -M <sub>2</sub>	+	-	++
	M <sub>1</sub> -M <sub>2</sub>	++	-	+*
Diastema length	C-P <sub>1</sub>	+	-	++
Mandible with	<i>i-i'</i>	++	-	+
	<i>k-k'</i>	++	-	+*
Mandible height <i>h-h'</i>	P <sub>1</sub>	++	-	+
	P <sub>2</sub>	++	-	+
	P <sub>3</sub>	++	-	+*
	P <sub>4</sub>	++	-	+*
	M <sub>1</sub>	++	-	+*
	M <sub>2</sub>	++	-	+*
Distance	<i>a-d</i>	+	-	++
	<i>e-e'</i>	++	-	+
Height crown	P <sub>4</sub>	+	-	++
	M <sub>1</sub>	+	-	++
Length	M <sub>1</sub>	+	-	++
Breadth	M <sub>1</sub>	++	-	+*
Length	M <sub>2</sub>	++	-	+*
Breadth	M <sub>2</sub>	++	-	+*



# 5 Discussion

In this chapter first some important critical remarks about the methods that were used and assumptions that were made that should be kept in mind when interpreting all results are presented. Subsequently, all results presented in Chapter 4 will be interpreted and conclusions will be drawn about the identity of the thirteen fossil North Sea specimens.

## 5.1 Assumptions and critical remarks

### 5.1.1 Comparative material

The initial comparative dataset consisted of *C. l. lupus* (Eurasian wolf), *C. l. familiaris* (dog), *Cuon alpinus* (dhole) and the genus *Vulpes* (true foxes) (3.2). *Vulpes* was immediately excluded as comparative genus, because a brief comparison of the 13 fossil North Sea specimens with *Vulpes vulpes* specimens resulted in very strong evidence that these fossil specimens are certainly not *Vulpes vulpes*. Hereby two assumptions were made: 1) the selection of fox specimens that was used in this comparison is representative of the species *Vulpes vulpes*, and 2) the 13 fossil North Sea specimens are neither other species of the genus *Vulpes* (such as *Vulpes lagopus*, the Arctic fox), because *Vulpes vulpes* is the largest *Vulpes* species (Wilson and Reeder, 2005) and all fossil North Sea specimens had already larger, longer, wider and thicker mandibles than this largest fox species. These assumptions are both valid to make. The brief comparison was only intended to confirm and observe personally what was already generally known from literature: true foxes can be distinguished from members of the genus *Canis* by their clearly smaller size, among other things (such as teeth, as observed in Chapter 3) (Wilson and Reeder, 2005).

The final comparative dataset consisted of *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* (3.2). Before measuring all parameters on all 100 Canidae specimens it was kept in mind that this selection made beforehand can determine the outcome. It is possible that a fossil North Sea specimen actually belongs to neither of these (sub)species and that the specimen thus cannot be assigned to any of the comparative (sub)species. It could also be, that the specimen still will be assigned to one of these three, because one of the comparative (sub)species is not excluded as possible identity for that specimen. However, this is a quite far-fetched and very critical remark that can be disregarded, because it is very reasonable to assume that the 13 fossil North Sea specimens are indeed *C. l. lupus*, *C. l. familiaris* or *Cuon alpinus* (as explained in Chapter 3 and indicated by all results in Chapter 4).

The comparative material consists of specimens that were available in the Canidae collection of NCB Naturalis (2.1.2). But, to what extent is this particular comparative dataset representative for the *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* populations of Northwestern Europe during the Pleistocene, with respect to:

#### *Sample sizes?*

The sample sizes of the three comparative (sub)species are not equally large (2.1.2). The sample sizes of *Cuon alpinus* and *C. l. lupus* are quite small (27 and 18 specimens respectively), because that was all material that was available for these two (sub)species in the Canidae collection of NCB Naturalis. This collection contained a huge amount of *C. l. familiaris* specimens, thus a selection had to be made, because there would not be enough time to measure all *C. l. familiaris* material present (this resulted in a sample size of 41 specimens). Moreover, it would not be logical to have an exceptionally large *C. l. familiaris* dataset compared to only 18 and 27 *C. l. lupus* and *Cuon alpinus* specimens. In 2.2.3 and 2.2.4 reasonably had to be assumed that these sample sizes are sufficiently large to be representative for the *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* populations of Northwestern Europe during the Pleistocene, in order to be able to draw conclusions with some confidence (which is a valid assumption to make for this particular study). In reality, the larger the sample size, the more representative the dataset.

#### *Subspecies?*

For *Cuon alpinus* only one species is recognized nowadays and the validity of many subspecies is doubtful (Durbin et al., 2008). The presence of several different subspecies (appendix II) is thus not really relevant, although it does indicate that this comparative dataset captures the variability within the *Cuon alpinus* species. The *C. l. lupus* dataset consists almost entirely of *C. l. lupus* LINNAEUS, 1758 (Eurasian wolf) specimens and is thus representative for the *C. l. lupus* population of Northwestern Europe. The *C. l. familiaris* dataset consists entirely of *C. l. familiaris* LINNAEUS, 1758 specimens and as many as possible dog breeds (to capture the *C. l. familiaris* variability in this selection). The *C. l. familiaris* dataset is also representative qua the subspecies that are included.

### Locality?

For *Cuon alpinus* the localities from where the 27 comparative specimens were acquired (appendix II) coincide with the current and historical distribution of *Cuon alpinus* (parts of Asia, Durbin et al., 2008). Qua locality the comparative *Cuon alpinus* sample is thus representative for this species in general. The *Cuon alpinus* sample cannot actually be representative for the *Cuon* population of Northwestern Europe, because it remains to be established whether *Cuon* was present there or not. Meanwhile, it is valid to compare the fossil specimens from the North Sea to *Cuon alpinus* specimens from Asia, since this is the type locality of *Cuon alpinus*. For *C. l. lupus* the localities of the comparative specimens are scattered throughout Europe and for three specimens (NMR86-88) the localities even coincide exactly with the finding place of two fossil North Sea specimens (NMR89 and NMR90, Southern Bight) (appendix II). The *C. l. lupus* sample is thus representative for the *C. l. lupus* population of Northwestern Europe. For *C. l. familiaris* the localities of the fossil specimens are scattered throughout the Netherlands and this part of the *C. l. familiaris* sample is thus representative for the *C. l. familiaris* population of Northwestern Europe. All recent specimens however come from Suriname and it is not known how these specimens were acquired exactly. This part of the comparative *C. l. familiaris* sample is probably less representative for this subspecies in Northwestern Europe during the Pleistocene. The two groups within the *C. l. familiaris* dataset were analyzed separately, because if we would treat the *C. l. familiaris* dataset as one group and compare the 13 fossil North Sea specimens to the entire sample for identification, we would make the assumption that the geographical variation within the *C. l. familiaris* subspecies is smaller than the variation between species, which we don't know. We observed in Chapter 4 that for most parameters the Dutch fossil part of the *C. l. familiaris* range is a subgroup within the recent part from Suriname (appendix VII). As expected, the fossil North Sea specimens that will be classified as *C. l. familiaris* always fell within this Dutch fossil subgroup, because the specimens coincide more qua age and locality with this group than with the recent specimens from Suriname.

### Age?

Almost all fossil specimens (1 *C. l. lupus* and 22 *C. l. familiaris* specimens) are of Weichselien age, which compares well to the estimated age of the fossil North Sea specimens (Late Pleistocene) (appendix II). For *Cuon alpinus* no fossil specimens were included in the comparative dataset, but it is assumed that there are no major differences between fossil and recent *Cuon* specimens and that the 13 fossil specimens, if they belong to this species, can be identified based on the comparative dataset of these recent *Cuon alpinus* specimens.

### Sex?

For all comparative specimens for which the sex is known the distribution male-female is approximately fifty-fifty (appendix II). Moreover, for *Cuon alpinus* there is no distinct sexual dimorphism (Durbin et al., 2008). We can thus reasonably assume that there is no (size) bias in the three comparative datasets due to possible sexual dimorphism.

In summary, the comparative dataset is (assumed to be) representative for the *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* populations that lived in Northwestern Europe during the Pleistocene with respect to sample size, subspecies, locality, age and sex.

### Hemimandibles

A remarkable observation in the comparative material is that all recent material consists of entire skulls (mandibles and maxillas) and that all fossil material (comparative and North Sea material) consists of only hemimandibles (appendix II). A possible explanation for this observation is that there is a bias in preservation and/or discovery of hemimandibles over maxillas. Mandibles are smaller, more easily detached from the skull and more easily transported to a sedimentary basin, where they can be preserved, than maxillas.

## 5.1.2 Specimen, sample and population ranges

### Assumptions

Conclusions about the identity of the fossil North Sea specimens will be based on the comparison of the specimen ranges with the sample and population ranges as presented in Chapter 4. Also for these three ranges several assumptions were made.

In the specimen ranges two assumptions are contained. The first assumption is that the differences with respect to the parameters are larger between (sub)species than between the left and right hemimandibles of specimens. This 'assumption' is valid, as results presented in 2.2.2 indicate. Moreover, specimen and sample ranges include more or less the effect of the difference between left and right hemimandibles, because the differences between the two hemimandibles (if present) are in the same order of size as the



measuring error, which is accounted for in the specimen and sample ranges. The second point of discussion for the specimen ranges is that not all parameters could be measured directly on each fossil North Sea specimen and some values were estimated using specimens of the comparative material (2.2.2). At first thought this method seems to be an example of 'reasoning in a circle': a fossil North Sea specimen is compared qualitatively to the comparative material and looks most like a certain *C. l. lupus* specimen for example. Then the value of that *C. l. lupus* specimen is used as estimate for the specimen range of that fossil North Sea specimen and compared to the comparative material (of which that same *C. l. lupus* specimen is part). Logically, the conclusion will be that the fossil North Sea specimen is most similar to *C. l. lupus*. On second thought this method is not that useless. There are valid reasons (qualitative comparisons of size and mandible ratio and other results that already indicated the identity of the specimen) why a certain comparative specimen was chosen to represent the value for that parameter for that fossil North Sea specimen. It is therefore very likely that the fossil North Sea specimen had a value for that parameter that is very similar to the estimated value and does not deviate much from it. Certainly when two comparative specimens were used as minimum and maximum value, it is almost certain that the fossil North Sea specimen was not smaller or bigger than is indicated by that specimen range (especially because specimen ranges are taken large). The estimated values for certain parameters of certain fossil North Sea specimens are thus a fairly good indicator of its size, although the values are still estimates. This means that the values should not be interpreted with the amount of significant digits in which the estimated values are given, but are still useful enough to give an indication of the identity of the fossil North Sea specimen.

Conclusions based on the comparison of specimen ranges with population ranges have a confidence interval of 95% (appendix VI) provided that the following assumptions are valid: 1) the sample sizes of the comparative *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* datasets are sufficiently large (meaning that the samples are representative of the amounts of variation concerning the subspecies, locality, age and sex int. al. that is present in the natural populations), 2) the sizes of the parameters used in this study are normally distributed in the *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* populations (appendix VI). The first assumption is valid, because of reasons explained in 5.1.1. The second assumption is valid, because it is generally known that many different naturally occurring distributions, including size, are normally distributed (appendix VI).

#### Values from literature

Additionally to the original sample and population ranges, new statistics, sample and population ranges were calculated for 6 parameters based on an extended dataset in which *Cuon alpinus* values from literature were included (2.2.5). It was not explained in the literature how these parameters were taken exactly and a slightly different way of measuring these parameters can result in different values for the same specimen. However, we can reasonably assume that the parameters as presented in Adam (1959) and Pérez Ripoll et al. (2010) would have had very similar values if they were measured according to the methods described in appendix IV. It is valid to compare the specimen ranges of the fossil North Sea specimens with the values obtained from the literature. Since the new dataset (including the values from the literature) is larger, it is a better representation of the entire natural *Cuon alpinus* population. Results obtained from the comparison to the new sample and population ranges are thus slightly more reliable. The new conclusions based on the extended comparative dataset should thus be taken as final conclusion.

#### Sexual dimorphism

Since the conclusions of all quantitative parameters are based on the typical size ranges obtained from the comparative datasets, we cannot tell the difference between a fossil North Sea specimen which is a dog (which is typically smaller than wolf) and a female wolf which shows extreme sexual dimorphism. Such a wolf would fall within the dog category and would be classified as dog based on its size. Since there are no clear differences between dog and wolf other than size, this possible problem cannot be solved. It has to be assumed that possible differences in sizes due to sexual dimorphism will not significantly influence the conclusions.

#### Deviating comparative specimens

In Chapter 4 we observed in the graphs that for some parameters one or two comparative specimens would deviate (have an extremely high or low value) from the rest of the specimens for that (sub)species. This is to be expected, because nature hardly ever represents itself in a linear manner. The 'deviation' of these specimens can thus already be explained by nature's variation and the fact that these specimens probably would fall perfectly within the comparative data cloud when sample sizes would have been larger. It is, however, interesting to see that for most of these deviating specimens their sex (possible dimorphism), subspecies (generally large or small) or breed (generally large or small) provides an additional explanation for their extremely large or small value (appendix II).

### 5.1.3 Peculiar SD vs. n trend

In Chapter 4 we observed a peculiar trend of the standard deviation vs. sample size of *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* for each quantitative parameter (see overview in table 4.41). For each parameter *C. l. familiaris* had the largest sample size (approximately 42 specimens), *Cuon alpinus* had a slightly smaller sample size (approximately 27 specimens) and *C. l. lupus* had the smallest sample size (approximately 18 specimens). One would expect that the (sub)species with the greatest sample size also has the greatest standard deviation, since the larger the dataset, the more different specimens are included, the more variation of the population is captured and the more representative the dataset is. But this was not the case. As depicted in table 4.41 *Cuon alpinus*, which has an average sample size, had the smallest standard deviation for each parameter, while *C. l. lupus*, the subspecies with the smallest sample size, always had the second largest or even (relatively) the largest standard deviation. *C. l. familiaris*, the subspecies with the largest sample size, had the largest standard deviation for most parameters, as expected. This means that there is less variation in the *Cuon alpinus* dataset with respect to all these parameters than in the *Canis* datasets and that the *C. l. lupus* dataset shows the highest amount of variation (the standard deviation represents the amount of dispersion within a dataset (appendix VI)). This can possibly be explained by the large geographical range of *C. l. lupus* in this dataset. The comparative *C. l. lupus* specimens were acquired at many localities throughout Europe, although not even all localities were known, while *Cuon alpinus* mainly comes from 1 location (Java) and *C. l. familiaris* from 2 locations (The Netherlands and Suriname) (appendix II). Additionally to this geographical range intraspecies variation can also cause the observed variation in the three comparative (sub)species: there are approximately 400 breeds of *C. l. familiaris*, while variation within *C. l. lupus* and *Cuon alpinus* is less (Nowak, 1999), which explains why the SD of *C. l. familiaris* is the largest for most parameters. But this peculiar SD vs. n trend could also be an effect of this particular comparative dataset: in that case the datasets of the three comparative (sub)species are not representative for the natural populations of *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* and extending these datasets with more specimens would immediately change the SD vs. n trend.

## 5.2 Mandible length

### 5.2.1 Length mandible *a-b* and *c-b*

Since parameters *a-b* and *c-b* have very similar results (4.1.1), they will be interpreted together and it will not be explicitly mentioned in each paragraph that conclusions hold true for both parameters. Only where parameters *a-b* and *c-b* do not have the same results, they will be mentioned separately.

#### 5.2.1.1 Comparative material

**x** *C. I. lupus* is a relatively large animal compared to *Cuon* and there is a huge variety within the *C. I. familiaris* subspecies, thus results of the mean values are as expected: *C. I. lupus* has the biggest mandible length, *Cuon alpinus* the smallest and *C. I. familiaris* has a mandible length in between (as described in 4.1.1.1). For all quantitative parameters it is expected that *C. I. lupus* has on average the biggest values, *Cuon alpinus* the smallest and that *C. I. familiaris* has intermediate values that sometimes will be closer to the *C. I. lupus* mean and other times to the *Cuon alpinus* mean (due to the high variety within this subspecies). Therefore, if results of parameters match the results described here, they will not be discussed into detail (to avoid unnecessary repetitions).

**Sample ranges** For the sample ranges results are as expected for *C. I. lupus* and *Cuon alpinus*, in that *C. I. lupus* has big mandible lengths, *Cuon alpinus* much smaller lengths and that they hardly overlap (4.1.1.1). Since *C. I. familiaris* is a subspecies of *C. I. lupus*, one would expect this subspecies to be more similar to *C. I. lupus* than to *Cuon alpinus*, another genus. But *C. I. familiaris* is much more similar to *Cuon alpinus* with respect to mandible length in that the *C. I. familiaris* range only partly overlaps with the *C. I. lupus* range and entirely with the *Cuon alpinus* range. *C. I. familiaris* mandibles can be just as small as *Cuon alpinus* mandibles. A probable reason for this observation is that *C. I. familiaris* has the largest dataset of the three comparative species and logically also shows the most variation in mandible sizes. A second explanation is that the *C. I. familiaris* dataset can be divided into two parts of recent specimens from Suriname and fossil Dutch specimens. The smallest *C. I. familiaris* specimens are all recent specimens from Suriname, while the Dutch fossil specimens form a distinct data cloud in the upper part of the scatter plot (fig. VII.1). (The recent part includes some specimens from the Netherlands, but the majority is from Suriname. The Dutch specimens also show the same distribution of mandible sizes as the specimens from Suriname, thus it is valid to refer to this part of the dataset as the recent part from Suriname.) Either the temporal (fossil vs. recent) or the geographical (Suriname vs. Netherlands) variable or both could, next to the large size of the dataset, be responsible for the large sample range of *C. I. familiaris*.

**Population ranges** Results are also as expected for the population ranges: *C. I. familiaris* still has a great range, but the *C. I. lupus* and *Cuon alpinus* ranges do not overlap for this range, where they did for the sample range (4.1.1.1). Thus based on the population ranges more conclusive statements can be made about the identity of the fossil North Sea specimens if they would fall within the overlap area for the sample range but only in one category for the population range. Results for the sample and population ranges are expected to be similar to the results of parameters *a-b* and *c-b* for all other quantitative parameters and will only be discussed into detail if they do not match the expected result.

**Trend lines** Trend lines are not the most reliable evidence based on which a specimen should be assigned to a species, because data can be quite scattered and trend lines would be meaningless. However for this parameter data points lie very nicely on a linear line and for a fixed value of *a-b* *Cuon alpinus* values consistently have a slightly lower value for *c-b* than *C. I. familiaris* (fig. VIII.1). Thus when a fossil North Sea specimen lies significantly above or below one of the three trend lines, this is additional evidence, but certainly not conclusive, for the identity of that specimen. Trend lines are thus merely used as a tool to better visualize the average position of the specimens of the data clouds of the three comparative species (which is already known from the absolute values in the tables) and to see to which species the fossil North Sea specimens compare best. The circumstantial evidence (trend lines and comparison of fossil specimens with means of the comparative material) is thus only used as additional tool and not as independent evidence.

#### 5.2.1.2 Fossil North Sea material

For 12 of the 13 fossil North Sea specimens, parameters *a-b* and *c-b* could not be measured directly on the specimen and values were estimated using specimens of the comparative material. All results that are discussed in this paragraph can be found in 4.1.1.2.

#### Specimen 534

Sample ranges indicate that 534 is *C. I. lupus*: specimen 534 falls within the upper part of the *C. I. lupus* ranges and clearly outside the *C. I. familiaris* and *Cuon alpinus* ranges. For *c-b* the minimum value of 534 coincides with the maximum value of the *C. I. familiaris* range and there could actually have been more overlap since this value is an estimate. But it is not likely that specimen 534 is *C. I. familiaris* since most of

the specimen range falls outside the *C. I. familiaris* range and since the qualitative description stated that 534 was very probably somewhat larger than the minimum value of its specimen range. Based on the sample ranges, 534 is most probably *C. I. lupus*.

Population ranges are more conclusive and also indicate that specimen 534 is *C. I. lupus*. Specimen 534 falls above the *C. I. familiaris* population range and very much above the *Cuon alpinus* range (the specimen range even partly exceeds the *C. I. lupus* range) for both *a-b* and *c-b*. This means that 97.7% of the *C. I. familiaris* and *Cuon alpinus* specimens of the entire population have smaller mandibles than specimen 534. There is only a 2.3% chance that 534 is *C. I. familiaris*, although the possibility that 534 is an exception (an extremely big *C. I. familiaris*) is still present (also because the value of 534 was an estimate and these percentages are not as strong an evidence as for specimens on which the parameter was taken directly). Due to the great distance between the *Cuon alpinus* maximum and the 534 specimen range minimum (38 mm) the possibility that 534 still might be a *Cuon alpinus* specimen is extremely small and negligible. The fact that specimen 534 falls partly outside (above) the *C. I. lupus* population range does not reduce the chance that 534 is *C. I. lupus*. According to the population ranges specimen 534 is very probably a *C. I. lupus* specimen.

The mean values of 534 of both *a-b* and *c-b* are most similar to the average *C. I. lupus* specimen and significantly less similar to *C. I. familiaris* and *Cuon alpinus*, which confirms that 534 looks more like *C. I. lupus* than *C. I. familiaris* and *Cuon alpinus*, although this is a circumstantial indication. The only purpose of this comparison is to get a general impression of the position of the specimen in the figures with respect to the comparative species, which gives an initial clue to the identity of the fossil North Sea specimen, but is no (independent) evidence for the identity of the specimen. An extremely small *C. I. lupus* specimen, for example, can be more similar to an average *C. I. familiaris* specimen than to *C. I. lupus*. The positions of the means thus only indicate whether a specimen, previously determined as a certain species by the sample and population ranges, has an typical value for that species or not. Specimen 534 plots exactly on the *C. I. lupus* trend line, far away from the *Cuon alpinus* and *C. I. familiaris* data clouds, which also supports the conclusion that 534 is a *C. I. lupus* specimen. These trend line interpretations are, like the means, also circumstantial evidence. Qualitative comparison of 534 with the comparative material indicated that 534 was much bigger than all comparative *C. I. familiaris* and *Cuon alpinus* specimens and that it only compared well in shape and size to *C. I. lupus*.

All evidence indicates that specimen 534 is very probably a *C. I. lupus* specimen, that there is only a 2.3% chance that it is *C. I. familiaris* and that 534 is certainly not *Cuon alpinus*.

### **Specimen 535**

The specimen range of 535 falls entirely within the sample ranges of *C. I. lupus* and *C. I. familiaris* and far outside the *Cuon alpinus* ranges for both *a-b* and *c-b*, which means that based on the sample ranges specimen 535 is *Canis*. The fact that specimen 535 falls within the upper part of the *C. I. familiaris* range does not decrease the possibility that 535 is *C. I. familiaris*. Based on these sample ranges only can be concluded that specimen 535 belongs to the genus *Canis*. Population ranges give the same result: 535 falls entirely within the sample ranges of *C. I. lupus* and *C. I. familiaris* and far outside the *Cuon alpinus* ranges (with 29 mm). This means that specimen 535 can be either of both *Canis* species, but that the chance that 535 is *Cuon alpinus* is probably even much less than 2.3% (for the same reason as explained for specimen 534). The mean value of 535 is most similar to the average *C. I. lupus* specimen and significantly less similar to *C. I. familiaris* and *Cuon alpinus*, which confirms that 535 looks more like *C. I. lupus* than *C. I. familiaris* and *Cuon alpinus*, although this is only circumstantial evidence. Specimen 535 plots very close to the *Canis* trend lines, above the *Cuon alpinus* data cloud, which confirms all stated above. Qualitative comparison of 535 with the comparative material indicated that 535 was much bigger than all comparative *Cuon alpinus* and almost all *C. I. familiaris* specimens and that it only compared well in shape and size to *C. I. lupus*.

All ranges indicate that 535 is very probably not *Cuon alpinus*, but a *Canis* specimen, although it cannot be concluded which subspecies. Circumstantial and quantitative evidence indicate that 535 is more dissimilar to *C. I. familiaris* and possibly is *C. I. lupus*.

### **Specimen 667**

Specimen 667 falls into the sample ranges of all comparative material, although only partly in the *C. I. lupus* range for *a-b* and partly in the *Cuon alpinus* range for *c-b*. Because in both cases the overlap is much less than the part of the range that does not overlap, the chance that 667 is *C. I. lupus* or *Cuon alpinus* would be slightly reduced, were it not that the specimen range of 667 was estimated. Based on the sample ranges 667 can be one of all comparative species. Population ranges are more conclusive: 667 falls outside the ranges of *C. I. lupus* and *Cuon alpinus* and within the range of *C. I. familiaris*. This means that there is only a 2.3% chance that 667 is *C. I. lupus* or *Cuon alpinus* and that 667 is very probably a *C. I. familiaris* specimen. The mean value of specimen 667 lies closest to the mean value of *C. I. familiaris*, which confirms the conclusion that 667 is a *C. I. familiaris* specimen (although circumstantial). Specimen 667 plots close to the trend lines of *Canis*, above all *Cuon alpinus* data points, which confirms that 667 is probably not *Cuon alpinus*, although this circumstantial evidence cannot differentiate between the two *Canis* species. The qualitative comparison

revealed that 667 does not look like *Cuon alpinus* and was too small to be compared to *C. l. lupus* specimens. This indicates that qualitatively 667 looks most like *C. l. familiaris*.

Specimen 667 is very probably a *C. l. familiaris* specimen: there is only a 2.3% chance that 667 is *C. l. lupus* or *Cuon alpinus*. Circumstantial and qualitative evidence confirm this conclusion.

### Specimen 1683

Specimen 1683 only falls in the *C. l. lupus* sample range and far outside the *C. l. familiaris* and *Cuon alpinus* ranges, which means that based on the sample range 1683 is very probably *C. l. lupus*. Population ranges give the same result as the sample ranges. Since the distance between the minimum value of the specimen range of 1683 and the maxima of the population ranges of *C. l. familiaris* and *Cuon alpinus* is very big, the chance that 1683 is a *Cuon alpinus* or *C. l. familiaris* specimen is probably even less than 2.3%. The estimated specimen range of 1683 falls even partly above the population range for *C. l. lupus*, while the actual mandible of 1683 probably was even larger. This means that 1681 is quite big, even for *C. l. lupus*. The mean value of specimen 1683 plots in the upper most part of the *C. l. lupus* range and is thus very dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens, which supports the conclusion that 1683 is *C. l. lupus*. The position of 1683 exactly on the *C. l. lupus* trend line, far above the *Cuon alpinus* and *C. l. familiaris* data clouds also is an indication, although circumstantial, that 1683 is a *C. l. lupus* specimen. From the qualitative comparison of 1683 with the comparative material can be concluded that specimen 1683 appears much bigger and heavily built than *Cuon alpinus* and *C. l. familiaris* specimens, and therefore is very probably a *C. l. lupus* specimen.

Based on the length of its mandible specimen 1683 is very probably a *C. l. lupus* specimen. With a probability of more than 97.7% we can conclude that 1683 is not *C. l. familiaris* or *Cuon alpinus*. Circumstantial and qualitative evidence confirm this conclusion.

### Specimen 2103

Specimen 2103 falls entirely within the sample ranges of *C. l. lupus* and *C. l. familiaris*, but also partly within the *Cuon alpinus* ranges, which means that based on the sample ranges 2103 could have been one of all comparative species. The fact that the specimen range slightly falls below the *C. l. lupus* sample range for *a-b* does not decrease the chance that 2103 is *C. l. lupus*, because the part of the range that overlaps is much bigger. The chance that 2103 is *Cuon alpinus* is also not reduced, although overlap of the specimen range of 2103 with the *Cuon alpinus* sample range is much smaller than the part of the specimen range that does not overlap. Qualitatively it was estimated that specimen 2103 could have had a slightly longer mandible than the minimum value of its specimen range. Since the overlap of the specimen range with the *Cuon alpinus* range is small, one would expect that the overlap is ignorable. But this specimen range was based on an estimated value, which means that possible overlap could have been more (or less). In this case the overlap (although small) is still significant. Based on the sample range we cannot exclude that specimen 2103 possibly is *Cuon alpinus* and all three comparative species are still possible. Population ranges indicate that specimen 2103 could have been either of the two *Canis* species, since the specimen range falls (partly) within those population ranges. That overlap is only partial for *C. l. lupus* does not decrease the possibility that 2103 is *C. l. lupus* (for reasons explained above). There is only a 2.3% chance that specimen 2103 is *Cuon alpinus* based on the population ranges.

Circumstantial evidence (means and trend lines) also indicates that 2103 is least similar to *Cuon alpinus* and most likely belongs to the genus *Canis*. Qualitative comparison of specimen 2103 with the comparative material indicated that 2103 is most similar in size and overall appearance to *C. l. familiaris*. Specimen 2103 appeared to have a larger mandible than all *Cuon alpinus* comparative material, a shorter mandible than most *C. l. lupus* material and looked fragile, like *C. l. familiaris*. These observations all indicate that based on the qualitative description 2103 is probably a *C. l. familiaris* specimen.

Quantitative evidence indicates that there is only a 2.3% chance that specimen 2103 is *Cuon alpinus* and circumstantial evidence confirms this conclusion. Specimen 2103 is thus very probably not a *Cuon alpinus*. Based on the quantitative evidence specimen 2103 can still either be *C. l. lupus* or *C. l. familiaris*. Only the qualitative description differentiates between the two *Canis* species and from that can be concluded that 2103 is more likely to be *C. l. familiaris* than *C. l. lupus* (although *C. l. lupus* cannot be entirely excluded as possibility).

### Specimen 2104

Sample ranges indicate that specimen 2104 can be *C. l. familiaris* or *Cuon alpinus*. For *c-b* specimen 2104 falls for most part in the *C. l. lupus* range, but based on parameter *a-b*, for which specimen 2104 falls outside the *C. l. lupus* sample range, we can conclude that 2104 is probably not *C. l. lupus*. For *a-b* 2104 falls entirely within the *Cuon alpinus* range and for *c-b* partly, thus *Cuon alpinus* cannot be excluded as possibility. Specimen 2104 falls within both *C. l. familiaris* ranges. Specimen 2104 can thus either be *C. l. familiaris* or *Cuon alpinus* based on the sample ranges. The specimen range of 2104 falls outside the population ranges of *C. l. lupus*, which means that there is only a 2.3% chance that 2104 is *C. l. lupus*.

Based on the population range of parameter *c-b* *Cuon alpinus* can also be excluded as possible species (2104 falls outside this range). Specimen 2104 falls within both *C. l. familiaris* ranges and is very probably a *C. l. familiaris* specimen. The mean value of specimen 2104 lies closest to the average *C. l. familiaris* specimen and is (much) less similar to average *Cuon alpinus* and *C. l. lupus* specimens, which supports the conclusion that 2104 is probably *C. l. familiaris*. Specimen 2104 plots exactly on the *C. l. familiaris* trend line, below the *C. l. lupus* data cloud and 'above' the *Cuon alpinus* specimens (for a fixed value of *a-b* 2104 has a slightly higher value for *c-b* than *Cuon alpinus*). This confirms above conclusion. Qualitatively specimen 2104 looks very similar to specimen 2103, which compared best to *C. l. familiaris* specimens. The same qualitative description as for 2103 holds true for 2104, which supports the conclusion that 2104 is *C. l. familiaris*. Specimen 2104 is very probably a *C. l. familiaris* specimen (there is only a 2.3% chance that it is *C. l. lupus* or *Cuon alpinus*). Circumstantial and qualitative evidence support this conclusion.

#### **Specimen 2196**

Specimen 2196 is a quite large hemimandible that is larger than all comparative *C. l. familiaris* and *Cuon alpinus* material and qua appearance looks most similar to *C. l. lupus* (2196 looks far too large and robust to be *Cuon alpinus* or *C. l. familiaris*). Based on the qualitative comparison of this specimen to the comparative material, it is very unlikely that 2196 is *Cuon alpinus* or *C. l. familiaris*. Since the same specimen range was used for 2196 as was used for specimen 1683, the results and also discussion for these results are the same for these two specimens. All conclusions made for specimen 1683 also hold true for 2196 (see discussion of 1683). 2196 is a *C. l. lupus* specimen.

#### **Specimen 2329**

All qualitative descriptions, results and discussion of the results of specimen 2329 are the same as for specimen 534 (see 534). Specimen 2329 is a *C. l. lupus* specimen.

#### **Specimen 2620**

All qualitative descriptions, results and discussion of the results of specimen 2620 are the same as for specimen 1683 (see corresponding paragraph). Specimen 2620 is a *C. l. lupus* specimen.

#### **Specimen 3219**

All qualitative descriptions, results and discussion of the results of specimen 3219 are the same as for specimen 2103 (see corresponding paragraph). Specimen 3219 is almost certainly not a *Cuon alpinus* specimen and is more likely to be *C. l. familiaris* than *C. l. lupus* (although *C. l. lupus* cannot be entirely excluded as possibility).

#### **Specimen 3293**

The specimen range of 3293 falls within the *C. l. lupus* sample range and outside the *Cuon alpinus* and *C. l. familiaris* ranges, from which can be concluded that based on the sample ranges specimen 3293 is *C. l. lupus*. For *c-b* the minimum value of 3293 coincided with the maximum value of the *C. l. familiaris* range and the specimen range was an estimate, thus overlap could even have been more. But specimen ranges were estimated in such a way that the fossil North Sea specimens were almost certainly larger than the minimum value of its specimen range and smaller than the maximum value, thus it is very probable that 3293 does not fall within the *C. l. familiaris* category. For the population ranges 3293 also only falls within the *C. l. lupus* range. 97.7% Of the *Cuon alpinus* and *C. l. familiaris* specimens are smaller than 3293 and there is only a 2.3% chance that 3293 is of these species. Based on the population ranges we can conclude that specimen 3293 is a *C. l. lupus* specimen. The mean value of 3293 is most similar to the average *C. l. lupus* specimen and significantly less similar to an average *Cuon alpinus* or *C. l. familiaris* specimen, which confirms the conclusion that 3293 is *C. l. lupus*. The position of 3293 in fig. VIII.1 (very close to the *C. l. lupus* trend line, above the *C. l. familiaris* and *Cuon alpinus* data clouds) also supports above conclusion. Qualitative evidence indicates that 3293 looks most similar to *C. l. lupus*: this specimen is bigger than all comparative *C. l. familiaris* and *Cuon alpinus* material and looks thick and robust unlike *C. l. familiaris* specimens. This description supports the conclusion that 3293 is *C. l. lupus*.

Specimen 3293 is almost certainly a *C. l. lupus* specimen (there is only a 2.3% chance that 3293 is *C. l. familiaris* or *Cuon alpinus*). Circumstantial and qualitative evidence support this conclusion.

#### **Specimen NMR89**

NMR89 falls within the sample ranges of both *Canis* species and outside the *Cuon alpinus* range. NMR89 is thus very probably not a *Cuon alpinus* specimen, but which of the two *Canis* species it is cannot be concluded from these ranges. Population ranges give the same result and conclusion: NMR89 is *Canis* (either one of the two species) and very likely not *Cuon alpinus* (for which there is only a 2.3% chance). NMR89 is more similar to the average *C. l. lupus* than *C. l. familiaris* specimen, but this indication is only

circumstantial. Also the trend lines only indicate that NMR89 is a *Canis* specimen, but do not differentiate between the two possible species.

There is only a 2.3% chance that NMR89 is *Cuon alpinus*, which is very likely not the case. NMR89 is almost certainly a *Canis* specimen, but based on the parameters *a-b* and *c-b* cannot be concluded whether NMR89 is *C. l. lupus* or *C. l. familiaris*.

### Specimen NMR90

Based on the sample ranges of *a-b* and *c-b* NMR90 could be either *Canis* or *Cuon alpinus*: the specimen range falls well within the sample ranges of *C. l. familiaris* and *Cuon alpinus* for *a-b* and within both *Canis* ranges for *c-b*. For *a-b* the specimen range of NMR90 only overlaps for 0.60 mm with the *C. l. lupus* sample range and for *c-b* only for 0.68 mm with the *Cuon alpinus* range. This would indicate that it is more likely that NMR90 is *C. l. familiaris* if the values were not estimated. But the values are estimates (the actual mandible length of NMR90 could deviate a few millimeters from this value) and do not entirely fall outside the *C. l. lupus* and *Cuon alpinus* ranges, which is no conclusive evidence for the identity of NMR90. NMR90 can thus still be both *Canis* and *Cuon alpinus*.

For *a-b* NMR90 falls only in the population range of *C. l. familiaris*; 97.7% of the *C. l. lupus* specimens has a larger mandible and 97.7% of the *Cuon alpinus* specimens has a shorter mandible than NMR90. There is only a 2.3% chance that NMR90 is *C. l. lupus* or *Cuon alpinus*, based on this parameter. Also for *c-b* NMR90 falls outside the *Cuon alpinus* range and within the *C. l. familiaris* range. NMR90 partly overlaps with the *C. l. lupus* population range, which means that based on parameter *c-b* the chance that NMR90 is *C. l. lupus* is still possible and slightly bigger than for *a-b*. NMR90 looks most like *C. l. familiaris* based on the population ranges, but, although there is only a small chance that NMR90 is *C. l. lupus* or *Cuon alpinus*, the possibility that NMR90 is an exception (extremely small *C. l. lupus* or extremely big *Cuon alpinus*) is still present. Again we have to keep in mind that the value of NMR90 was an estimate and that these percentages are not as strong evidence as for specimen on which the parameter was taken directly.

The mean values of NMR90 of both *a-b* and *c-b* are most similar to the average *C. l. familiaris* specimen and significantly less similar to *C. l. lupus* and *Cuon alpinus*, which indicates that NMR90 looks more like *C. l. familiaris* than *C. l. lupus* and *Cuon alpinus*, but this is only a circumstantial indication. Specimen NMR90 plots exactly on the *C. l. familiaris* trend line and is positioned above all *Cuon alpinus* specimens (fig. VIII.1), which also is a circumstantial indication that NMR90 is more similar to *C. l. familiaris* than to *Cuon alpinus*. NMR90 has other mandible ratios than all comparative *Cuon alpinus* specimens: the mandible length of NMR90 is too long compared to other mandible features. The fossil North Sea specimen also looks fragile and quite small compared to *C. l. lupus* specimens. NMR90 visibly does not compare well to *Cuon alpinus* or *C. l. lupus* and qualitatively can best be assigned to *C. l. familiaris*.

In Chapter 4 it was stated that NMR90 was slightly bigger than comparative *C. l. familiaris* specimen 18051 and comparable in size to specimen 34601. Thus it was expected that specimen 18051 would have the smallest mandible size and 34601 the biggest. But specimen 18051 gave the maximum and specimen 34601 the minimum value for the NMR90 specimen range for *a-b*. It could be that the entire hemimandible of 18051 appeared smaller than NMR90, but that the specific parameter 'length mandible' was actually slightly smaller. More probably this paradox is the result of the measuring error. The difference between the two comparative specimens (0.51 mm) is smaller than the measuring error (0.91 mm), which means that, if specimens 18051 and 34601 would be measured again, it very well could be that 18051 would then have the largest value and 34601 the lowest. For *c-b* 18051 did give the minimum and 34601 the maximum value for the NMR90 specimen range. NMR90 was estimated to be slightly bigger than this minimum value and NMR90 only partly overlapped with the *Cuon alpinus* sample range (while in this NMR90 specimen range the measuring error also already is included), thus one could argue that NMR90 does probably not fall within the *Cuon alpinus* sample range (but this would not be that reliable since the NMR90 specimen range was estimated).

Qualitative descriptions already indicated that NMR90 is most similar to *C. l. familiaris* and the quantitative results confirm this: there is only a 2.3% chance that NMR90 is *C. l. lupus* or *Cuon alpinus*.

## 5.2.2 Alveolar lengths $P_1-M_2$ , $P_4-M_1-M_2$ (and $M_1-M_2$ )

Primarily results of parameters  $P_1-M_2$  and  $P_4-M_2$  will be discussed in this paragraph and were referred to 'alveolar lengths' only  $P_1-M_2$  and  $P_4-M_2$  will be meant. Only for specimen 535 parameter  $M_1-M_2$  is discussed. Since 'Alveolar length' parameters  $P_1-M_2$  and  $P_4-M_2$  have very similar results (4.1.2), they will be interpreted together and it will not be explicitly mentioned in each paragraph that conclusions hold true for both parameters. Only where the parameters do not have the same results, they will be mentioned separately.

### 5.2.2.1 Comparative material

As already stated in the paragraph of parameter *a-b*, it is expected for all quantitative parameters that *C. l. lupus* has on average the biggest values, *Cuon alpinus* the smallest and that *C. l. familiaris* has intermediate values that sometimes will coincide more with the *C. l. lupus* data cloud and other times more with the *Cuon*

*alpinus* data points. Explanations and general statements about the interpretation of means, sample and population ranges, distinction between fossil specimens from the Netherlands and recent specimens from Suriname and trend lines were already given in that paragraph and hold true for all results that are similar to those of *a-b*. Since all results of the alveolar lengths match the expected result and there are no extraordinary observations in the results of these parameters (4.1.2.1), there is no need repeat interpretations of this. See 5.2.1.1.

### 5.2.2.2 Fossil North Sea material

#### Specimen 535

For specimen 535 results are from parameter  $M_1-M_2$  (4.1.3). Results for specimen 535 are very conclusive: the specimen range of 535 falls entirely within the sample and population ranges of *C. l. lupus* and entirely outside (above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* for parameter  $M_1-M_2$ , which means that specimen 535 is almost certainly a *C. l. lupus* specimen. 97.7% Of the *C. l. familiaris* and *Cuon alpinus* specimens of their populations have smaller alveolar ( $M_1-M_2$ ) lengths than specimen 535, thus there is only a 2.3% chance that 535 is one of these species. The mean value of 535 is most similar to the average *C. l. lupus* specimen and less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens, which confirms (although circumstantially) the conclusion that 535 is *C. l. lupus*. Based on previous parameters could not be established yet which *Canis* species specimen 535 was, but based on parameter  $M_1-M_2$  we now can conclude that 535 is *C. l. lupus*.

From this point on only results of  $P_1-M_2$  and  $P_4-M_2$  will be discussed (4.1.2.2).

#### Specimen 667

Specimen 667 can be either *C. l. familiaris* or *Cuon alpinus*, but not *C. l. lupus*. Specimen 667 falls within the sample and population ranges of *Cuon alpinus* and *C. l. familiaris* and outside (below) the population ranges of *C. l. lupus*. This means that 97.7% of the specimens of the entire *C. l. lupus* population has smaller alveolar lengths than specimen 667. There is thus only a 2.3% chance that specimen 667 belongs to *C. l. lupus*, but, although this chance is very small, the possibility that specimen 667 is an exception (an extremely small *C. l. lupus*) is still present. Mean values are also not conclusive about the identity of specimen 667. For both parameters specimen 667 is most dissimilar to the average *C. l. lupus* specimen, which confirms, although circumstantially, that specimen 667 probably does not belong to this species. But parameter  $P_1-M_2$  indicates that 667 is most similar to the average *C. l. familiaris* specimen, while parameter  $P_4-M_2$  indicates that 667 is most similar to the average *Cuon alpinus* specimen. In fig. 4.4 specimen 667 plots in between the *Cuon alpinus* and *C. l. familiaris* means thus even from this circumstantial evidence cannot be concluded whether 667 belongs to *Cuon alpinus* or *C. l. familiaris*. Specimen 667 lies closest to the trend line of *C. l. familiaris*, far away from *C. l. lupus* specimens, but does not plot outside the *Cuon alpinus* data cloud and is not positioned significantly far away from *Cuon alpinus* data points. This means that based on the position of 667 in fig. VIII.2 and the trend lines neither *Cuon alpinus* nor *C. l. familiaris* can be excluded as possibility for the identity of specimen 667. There is only a 2.3% chance that specimen 667 is *C. l. lupus*, thus 667 very probably does not belong to this species. Based on the alveolar lengths cannot be concluded whether 667 belongs to *Cuon alpinus* or *C. l. familiaris*.

#### Specimen 1683

Based on the alveolar lengths can be concluded that specimen 1683 can only be a *C. l. lupus* specimen; the specimen range of 1683 only falls within the *C. l. lupus* sample and population ranges and far outside the *Cuon alpinus* and *C. l. familiaris* ranges. This means that there is only a 2.3% chance that 1683 is a *Cuon alpinus* or *C. l. familiaris* specimen (with extremely large alveolar lengths). Specimen 1683 also plots in the upper part of fig. VIII.2 at a great distance from the *Cuon alpinus* and *C. l. familiaris* means and data clouds and very close to the *C. l. lupus* trend line. This circumstantial evidence supports the conclusion that 1683 is a *C. l. lupus* specimen. It can thus be concluded that specimen 1683 is almost certainly a *C. l. lupus* specimen and not *C. l. familiaris* or *Cuon alpinus* (for which there is only a 2.3% chance).

#### Specimen 2103

Comparison of the specimen range of 2103 with the sample ranges indicates that 2103 probably is not a *C. l. lupus* or *Cuon alpinus* specimen. Specimen 2103 falls entirely within the *C. l. lupus* sample range for parameter  $P_1-M_2$ , but entirely outside (below) this range for parameter  $P_4-M_2$ . Based on parameter  $P_4-M_2$  *C. l. lupus* can thus be excluded as possibility. Specimen 2103 falls inside the *Cuon alpinus* sample range for  $P_4-M_2$ , but outside (above) this range for  $P_1-M_2$ . Based on parameter  $P_1-M_2$  *Cuon alpinus* can be excluded as possibility. Both parameters do not give the same possibilities for what species specimen 2103 can be, nor do they exclude the same species (according to the sample ranges of parameter  $P_1-M_2$  specimen 2103 can still be *C. l. familiaris* or *C. l. lupus*, but according to the sample ranges of parameter  $P_4-M_2$  2103 can still be *C. l. familiaris* or *Cuon alpinus*). But from the combination of interpretations of both parameters can be



concluded that specimen 2103 probably is a *C. l. familiaris* specimen. Population ranges confirm this conclusion; 2103 falls outside the population range of *C. l. lupus* for parameter  $P_4-M_2$ , outside the *Cuon alpinus* population ranges for both parameters and inside the *C. l. familiaris* ranges. This means that 97.7% of the *C. l. lupus* and *Cuon alpinus* specimens of their entire natural populations have smaller respectively larger alveolar lengths than specimen 2103 and that the chance that 2103 is one of these two species is very small. Circumstantial evidence (means and trend lines) also supports the conclusion that 2103 is very probably a *C. l. familiaris* specimen; the mean value of specimen 2103 is most similar to the average *C. l. familiaris* specimen, plots closest to the trend line of *C. l. familiaris* and has a relatively small  $P_4-M_2$  length compared to its  $P_1-M_2$  length in comparison to *Cuon alpinus* and *C. l. lupus* data points. Specimen 2103 is thus almost certainly a *C. l. familiaris* specimen (there is only a 2.3% chance that 2103 is *Cuon alpinus* or *C. l. lupus*).

#### **Specimen 2104**

Also for this parameter the combination of both 'Alveolar length' parameters excludes both *C. l. lupus* and *Cuon alpinus* as possible identities for specimen 2104. The specimen range of 2104 falls within both *Canis* sample ranges of parameter  $P_1-M_2$ , but outside the *Cuon alpinus* sample range, which means that 2104 probably is not a *Cuon alpinus*. For parameter  $P_4-M_2$  2104 falls within the *C. l. familiaris* and *Cuon alpinus* sample ranges, but outside the *C. l. lupus* sample range, thus based on this parameter can be concluded that 2104 is probably not a *C. l. lupus* specimen. Population ranges confirm this conclusion. Specimen 2104 falls for most part within the *C. l. lupus* population range of parameter  $P_1-M_2$ , which does not reduce the chance that 2104 is *C. l. lupus*, but specimen 2104 falls entirely outside the *C. l. lupus* population range for parameter  $P_4-M_2$ , based on which we can conclude that specimen 2104 is almost certainly not *C. l. lupus* (for which the chance is only 2.3%). Based on the population range of parameter  $P_4-M_2$  2104 could still be *Cuon alpinus*, because the specimen range of 2104 falls entirely within that range, but parameter  $P_1-M_2$  excludes this possibility; specimen 2104 falls entirely outside the *Cuon alpinus* population range of this parameter, which means that there is only a 2.3% chance that specimen 2104 is *Cuon alpinus*. Circumstantial evidence also points towards *C. l. familiaris* as most probable candidate for the identity of specimen 2104: the mean value of specimen 2104 is most similar to the average *C. l. familiaris* specimen and plots closest to the trend line of *C. l. familiaris*. Specimen 2104 is thus almost certainly a *C. l. familiaris* specimen and there is only a 2.3% chance that 2104 is *C. l. lupus* or *Cuon alpinus*.

#### **Specimen 2196**

From fig. 4.4 and the sample and population ranges for both parameters, becomes very clear that specimen 2196 is a very large hemimandible, which has very large alveolar lengths compared to *C. l. familiaris* and *Cuon alpinus*. The specimen range of 2196 falls far outside the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* for both parameters, which means that 97.7% of the natural *Cuon alpinus* and *C. l. familiaris* populations have smaller alveolar lengths than specimen 2196 and that 2196 is very likely a *C. l. lupus* specimen. Specimen 2196 falls within the population ranges of both parameters and even above the sample range of  $P_4-M_2$ , which means that even for *C. l. lupus* 2196 has quite large alveolar lengths. As was already obvious from fig. VIII.2, 2196 plots in the upper part of the graph, far above *Cuon alpinus* and *C. l. familiaris* data clouds, means and trend lines, thus this circumstantial evidence supports the conclusion that specimen 2196 is almost certainly a *C. l. lupus* specimen.

#### **Specimen 2329**

Specimen 2329 falls entirely within the *C. l. lupus* sample and population ranges and entirely outside (above) the *C. l. familiaris* and *Cuon alpinus* sample and population ranges for both parameters, which means that there is only a 2.3% chance that 2329 is *C. l. familiaris* or *Cuon alpinus*. Specimen 2329 is most similar to the average *C. l. lupus* specimen, very dissimilar to *C. l. familiaris* and *Cuon alpinus* and plots closest to the *C. l. lupus* trend line, far away from the *C. l. familiaris* and *Cuon alpinus* data clouds, which is circumstantial evidence that supports the conclusion that specimen 2329 is almost certainly a *C. l. lupus* specimen.

#### **Specimen 2620**

Specimen 2620 only falls within the sample and population ranges of *C. l. lupus* and (far) outside those ranges of *C. l. familiaris* and *Cuon alpinus*, which means that 97.7% of the *Cuon alpinus* and *C. l. familiaris* specimens in their population have smaller alveolar lengths than specimen 2620. This fossil specimen is even quite large for a *C. l. lupus* specimen as is obvious from the fact that its specimen range falls above the sample range of parameter  $P_1-M_2$ . Evidently also in this case the circumstantial evidence (mean and trend lines) support the conclusion that specimen 2620 is most similar *C. l. lupus*, since 2620 plots in the upper part of fig. VIII.2 far away from the *C. l. familiaris* and *Cuon alpinus* data clouds. There is only a 2.3% chance that specimen 2620 is a *C. l. familiaris* or *Cuon alpinus* specimen and 2620 almost certainly belongs to *C. l. lupus*.

### **Specimen 3219**

Specimen 3219 falls entirely outside the sample and population ranges of *Cuon alpinus*, which means that there is only a 2.3% chance that 3219 is *Cuon alpinus* and that 3219 is thus very probably a *Canis* specimen. But 3219 falls entirely within the sample and population ranges of both *Canis* species, thus based on these two 'Alveolar length' parameters it cannot be concluded whether specimen 3219 belongs to *C. l. lupus* or *C. l. familiaris*. The specimen range of 3219 only falls in the lower parts of the sample and population ranges of *C. l. lupus*, but this does not reduce the chance of 3219 being this species. The mean value of 3219 indicates that this fossil specimen is more similar to the average *C. l. familiaris* specimen than to the average *C. l. lupus* specimen, but based on this circumstantial evidence one cannot conclude that 3219 is thus *C. l. familiaris*. Specimen 3219 plots slightly closer to the *C. l. lupus* trend line, but not outside either of both *Canis* data clouds, thus based on this (weak) indication no conclusions can be based about the identity of specimen 3219. Specimen 3219 is thus almost certainly not a *Cuon alpinus* specimen (for which is only 2.3% chance), but a *Canis* specimen, although based on alveolar lengths  $P_1-M_2$  and  $P_4-M_2$  cannot be concluded which *Canis* species.

### **Specimen 3293**

Results are very conclusive about the identity of specimen 3293: the specimen range falls entirely within the sample and population ranges of *C. l. lupus* and entirely outside (above) the *C. l. familiaris* and *Cuon alpinus* sample and population ranges, which means that 3293 is almost certainly a *C. l. lupus* specimen and that there is only a 2.3% chance that this fossil specimen is *C. l. familiaris* or *Cuon alpinus*. Circumstantial evidence (the mean value of specimen 3293 is most similar to the average *C. l. lupus* specimen and plots very close to the *C. l. lupus* trend line, far above the *C. l. familiaris* and *Cuon alpinus* data clouds) supports this conclusion.

### **Specimen NMR89**

Also for this fossil North Sea specimen result are conclusive: the specimen range of NMR89 falls entirely within the sample and population ranges of *C. l. lupus* and entirely outside (above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* for both parameters. This means that 97.7% of the *C. l. familiaris* and *Cuon alpinus* specimens of their populations have smaller alveolar lengths than NMR89 and that there is thus only a 2.3% chance of NMR89 being one of these species. The mean value of NMR89 is most similar to the average *C. l. lupus* specimen and plots closest to the *C. l. lupus* trend line in the upper part of fig. VIII.2, which confirms, although only circumstantially, that NMR89 is almost certainly a *C. l. lupus* specimen.

### **Specimen NMR90**

The specimen range of NMR90 falls only slightly outside the sample ranges of *C. l. lupus* and *Cuon alpinus*, but there is no overlap. NMR90 also falls entirely outside the population ranges of these species and side the *C. l. familiaris* ranges, which means that there is only a 2.3% chance that NMR90 is *C. l. lupus* or *Cuon alpinus*. NMR90 is also most similar to the average *C. l. familiaris* specimen, which (although circumstantially) supports the conclusion that NMR90 is almost certainly a *C. l. familiaris* specimen.

### **Values from literature**

For the parameters 'Alveolar length  $P_1-M_2$  and  $M_1-M_2$ ' values of six *Cuon alpinus* specimens from literature were added to the comparative dataset and the fossil North Sea specimens were compared to the newly calculated sample and population ranges (table IX.1, IX.2 and appendix VII).

#### *Following interpretations discuss the results of parameter $P_1-M_2$*

Comparison of the specimen range of specimen 667 with the new sample and population ranges indicated that this specimen still falls entirely inside the sample and population ranges of *Cuon alpinus*, which means that 667 still can be this species. Specimens 1683, 2196, 2329, 2620, 3293 and NMR89 still fall entirely outside the *Cuon alpinus* sample and population ranges, thus the extended dataset confirms that it is very unlikely that these specimens are *Cuon alpinus* (for which there is only a 2.3% chance). For specimens 2103, 2104 and 3219 the results of the new comparison were different: the specimen ranges fell entirely outside the *Cuon alpinus* sample and population ranges for the original dataset, but fall entirely within the new *Cuon alpinus* ranges. The original conclusion for these three specimens was that there is only a 2.3% chance that these specimens are *Cuon alpinus*, but based on the new, larger *Cuon alpinus* comparative dataset we have to conclude that this chance is much larger and that specimens 2103, 2104 and 3219 can very well be *Cuon alpinus*.

*Following interpretations discuss the results of parameter  $M_1-M_2$*

For specimens 535, 667, 1683, 2104, 2196, 2329, 2620, 3293 and NMR89 the previous results and thus interpretations were confirmed. Specimens 667 and 2104 fall entirely inside the *Cuon alpinus* sample and population ranges of the extended comparative dataset, which means that also based on the new dataset these two specimens still can belong to *Cuon alpinus*. Specimens 535, 1683, 2196, 2329, 2620, 3293 and NMR89 fall entirely outside the *Cuon alpinus* sample and population ranges, which confirms that these specimens are very likely not *Cuon alpinus* (for which there is a chance of only 2.3%). For specimen 2103 results were not confirmed: 2103 originally fell partly outside the *Cuon alpinus* sample range and entirely outside the corresponding population range, but falls entirely within the new *Cuon alpinus* sample and population ranges. This means that based on the extended *Cuon alpinus* dataset specimen 2103 still could be *Cuon alpinus*. Also for specimen NMR90 the conclusion is different than before: originally NMR90 fell outside the *Cuon alpinus* sample and population ranges, but falls entirely within both new *Cuon alpinus* ranges, which means that also NMR90 could be *Cuon alpinus* based on the extended dataset. For specimen 3219 results are slightly different, but this does not change the final conclusion: originally the specimen fell entirely outside both *Cuon alpinus* ranges and it still falls outside the new *Cuon alpinus* population range, but falls within the new *Cuon alpinus* sample range. Based on the new sample range 3219 can thus still be *Cuon alpinus*, but based on the population range we can still conclude that there is only a 2.3% chance that 3219 is *Cuon alpinus*.

## 5.2.3 Mandibular diastema length

### 5.2.3.1 Diastema length C-P<sub>1</sub>

#### 5.2.3.1a Comparative material

In almost all *Cuon alpinus* of the dataset used for this study mandibular diastemata between C-P<sub>1</sub> were present, while it was expected that in *Cuon alpinus* diastemata would be absent in a significant amount of the specimens (based on a statement of García and Arsuaga (1998), 4.1.4.1a). This led to the hypothesis that not only the absence of diastemata is an indication for the relative shortness of the mandibles of *Cuons*, but that, when diastemata are present in *Cuon alpinus*, they will be reduced in size compared to *Canis*. Results indicated that this was indeed the case: almost all *Cuon alpinus* specimens possessed diastemata between their canines and first premolars, which, with an average length of 3.10 mm, are about half the length of diastemata of *Canis* specimens. Thus, although there was much overlap of the sample and population ranges of comparative material, the hypothesis is confirmed: mandibular diastema length is indeed a species indicator. For this parameter the *C. l. familiaris* mean lay closer to the *C. l. lupus* mean than to the *Cuon alpinus* mean, which is in contrast to the previous parameters, but more logical, since *C. l. familiaris* is a subspecies of *C. l. lupus* and taxonomically thus more similar to *C. l. lupus* than to *Cuon alpinus*, another genus. Further results of C-P<sub>1</sub> are as expected and interpretations will not be repeated (see 5.2.1.1 for a general interpretation of comparative results).

#### 5.2.3.1b Fossil North Sea material

All results that are discussed in this paragraph can be found in 4.1.4.1b.

#### Specimen 667

Based on diastema length C-P<sub>1</sub> cannot be concluded to which *Canis* species specimen 667 belongs. Specimen 667 falls outside (above) the population range of *Cuon alpinus*, which means that there is only a 2.3% chance that 667 is *Cuon alpinus*, but falls inside the sample and population ranges of both *Canis* specimens. The mean value of specimen 667 for this parameter is most similar to the average *C. l. familiaris* specimen, which would be a circumstantial indication that 667 looks more like *C. l. familiaris*, but the mean is also quite similar to the average *C. l. lupus* specimen. Based on the C-P<sub>1</sub> diastema length can thus only be concluded on species level, that specimen 667 belongs to either two of both *Canis* species, but is almost certainly not a *Cuon alpinus*.

#### Specimen 1683

For this specimen evidence is more conclusive. Based on the sample ranges specimen 1683 could still be either of both *Canis* species, since 1683 falls within the sample ranges of both *C. l. lupus* and *C. l. familiaris*. But 1683 falls entirely outside (above) the population ranges of *C. l. familiaris* and *Cuon alpinus*, which means that 97.7% of the *C. l. familiaris* and *Cuon alpinus* specimens of their entire population have smaller diastemata between their canine and first premolar and that the chance that 1683 is *C. l. familiaris* or *Cuon alpinus* is thus very small. The mean value of specimen 1683 for this parameter is most similar to the average *C. l. lupus* specimen, which confirms the conclusion that 1683 is almost certainly a *C. l. lupus* specimen.

### **Specimen 2103**

Specimen 2103 falls entirely within the sample and population ranges of both *Canis* species, thus based on this parameter cannot be concluded whether 2103 is *C. l. lupus* or *C. l. familiaris*; chances are equal. Circumstantial evidence (the mean value of specimen 2103 for this parameter is most similar to the average *C. l. lupus* specimen) is not strong enough to base a conclusion on. Specimen 2103 is almost certainly not a *Cuon alpinus*, because the specimen range of 2103 falls entirely outside (above) the *Cuon alpinus* population range.

### **Specimen 2104**

For specimen 2104 a similar story holds true as for the previous one: specimen 2104 falls entirely inside the sample and population ranges of both *Canis* species, thus based on diastema length C-P<sub>1</sub> cannot be concluded whether 2104 is *C. l. lupus* or *C. l. familiaris*. The specimen range of 2104 falls entirely outside (above) the *Cuon alpinus* sample and population ranges, which means that there is only a 2.3% chance that 2104 is *Cuon alpinus*. Again circumstantial evidence (the mean value of specimen 2104 for this parameter is most similar to the average *C. l. lupus*) is not conclusive. Based on C-P<sub>1</sub> can be concluded that specimen 2104 is almost certainly not a *Cuon alpinus*, but a *Canis* specimen.

### **Specimens 2196 and 2329**

Both specimens plot close to specimen 2104 in fig. 4.6, show the same result and consequently have the same interpretation: both specimens fall entirely inside the sample and population ranges of both *Canis* species and entirely outside (above) the *Cuon alpinus* sample and population ranges. This means that both specimens are very likely not *Cuon alpinus*, but either one of both *Canis* specimens: there is only a 2.3% chance that specimens 2196 and 2329 are *Cuon alpinus*, based on diastema length C-P<sub>1</sub>. The mean values of both specimens are most similar to the average *C. l. lupus* specimen, which (circumstantially) indicates that the two fossil North Sea specimens look more like *C. l. lupus*, but based on this no conclusive statement can be made about the identity of specimens 2196 and 2329.

### **Specimens 2620 and 3219**

These two fossil North Sea specimens both fell entirely within the *Canis* sample and population ranges, (partially) within the *Cuon alpinus alpinus* sample ranges, but entirely outside corresponding population ranges. This means that both specimens are almost certainly not *Cuon alpinus*, but either one of both *Canis* specimens: there is only a 2.3% chance that specimens 2620 and 3219 are *Cuon alpinus*, based on diastema length C-P<sub>1</sub>. The mean values of both specimens are most similar to the average *C. l. lupus* specimen, which (circumstantially) indicates that the two fossil North Sea specimens look more like *C. l. lupus* than *C. l. familiaris*, but this is only a circumstantial indication. Based on the 'Diastema length' C-P<sub>1</sub> cannot be determined whether these two fossil specimens are *C. l. familiaris* or *C. l. lupus*.

### **Specimen 3293**

Results are less conclusive for specimen 3293 for this parameter as for previous parameters. Specimen 3293 falls entirely within the sample and population ranges of *C. l. familiaris* and *C. l. lupus*, thus, although the mean value of specimen 3293 for this parameter is most similar to the average *C. l. familiaris* specimen, based on diastema length C-P<sub>1</sub> cannot be concluded whether 3293 is a *C. l. lupus* or *C. l. familiaris* specimen. This fossil specimen falls outside (above) the population range of *Cuon alpinus*, which means that 3293 is almost certainly not a *Cuon alpinus* specimen.

## **5.2.3.2 Diastemata lengths between P<sub>2</sub>-P<sub>3</sub> and/or P<sub>3</sub>-P<sub>4</sub>**

### **5.2.3.2a Comparative material**

Results that are discussed can be found in 4.1.4.2a. Diastemata between premolars occur in a significant number of specimens of all comparative species (93%, 78% and 56% for respectively *C. l. familiaris*, *C. l. lupus* and *Cuon alpinus*). From just the information whether diastemata are present between the premolars no conclusions can be drawn about the identity of the fossil specimens. What might or might not be concluded from the absence of diastemata is not relevant, since all fossil North Sea specimens for which this parameter could be taken have diastemata between their premolars.

Sizes of diastemata are more conclusive. The presence of large diastemata between premolars is an indication that the specimen is not likely a *Cuon alpinus* specimen. There was only one *Cuon alpinus* specimen in which a large diastema occurred between premolars (which is equivalent to 4% of the *Cuons*), compared to approximately 50% of the *C. l. lupus* and *C. l. familiaris* specimens. When a large diastema is encountered in a fossil North Sea specimen, the chance is thus larger that this specimen belongs to the genus *Canis* instead of *Cuon alpinus* (based on this dataset). But the possibility that a specimen with a large diastema between its premolars is a *Cuon alpinus* cannot be entirely excluded. Presence of a large diastema is thus not conclusive evidence about the identity of a fossil specimen, solely an indication.

Small diastemata occur in a significant number of specimens of all comparative material (in 52% of the *Cuon alpinus* specimens, 45% of the *C. l. familiaris* specimens and 28% of the *C. l. lupus* specimens). Since these are all significant amounts and the presence of small diastemata is not rare for any of the comparative species, nothing can be concluded from the presence of these diastemata.

In summary: only the presence of large diastemata provides information about the identity of the fossil North Sea specimens and only on genus level (*Canis* or *Cuon*). It indicates that the specimen more probably belongs to the genus *Canis* than to *Cuon*, because the presence of large diastemata in *Cuon* is quite rare (this is certainly not conclusive evidence).

### 5.2.3.2b Fossil North Sea material

#### Specimens 534, 535 and NMR90

These three specimens miss a large anterior part of their hemimandible, thus presence of diastemata could not be determined (table 4.9, 4.1.4.2b).

#### Specimen 667

Specimen 667 has small diastemata between its premolars, but based on this information no conclusion can be drawn about the identity of this specimen, since small diastemata occur in a significant number of specimens of all three comparative species (table 4.9).

#### Specimens 1683, 2103, 2104, 2196, 2329, 2620, 3219, 3293 and NMR89

These fossil North Sea specimens have large diastemata between their premolars, which means that they are likely not *Cuon alpinus* specimens, because *Cuon alpinus* mandibles are smaller than those of *Canis* specimens and the occurrence of large diastemata between the premolars in *Cuon alpinus* is quite rare (table 4.9). But this indication towards a *Canis* identity is, however, far from conclusive; it only confirms results obtained by previous parameters.

## 5.2.4 Mental foramina

### 5.2.4.1 Comparative material

Results can be found in 4.1.5.1. The observation of a middle mental foramen positioned below  $P_1$ - $P_2$  is a strong indication for the genus *Canis*, since in this comparative dataset the middle foramen was never observed on this position in *Cuon alpinus*. The middle mental foramen occurs below  $P_1$ - $P_2$  in similar percentages for both *Canis* species, thus based on this position one cannot differentiate between *C. l. familiaris* and *C. l. lupus*. The middle mental foramen occurs below  $P_2$  anterior in similar percentages for all three comparative species, thus this particular position of the foramen is not indicative for a certain species.

In *C. l. lupus* and *C. l. familiaris* the middle mental foramen is never positioned below  $P_2$ , which is a strong indication that a specimen in which this position of the foramen is observed is *Cuon alpinus*; this position occurs quite often (56%) in *Cuon alpinus*. The middle mental foramen is rarely positioned below  $P_2$  posterior in all three comparative species and never in the fossil North Sea material, thus it is not relevant what this position might indicate. Summarized, the position of the middle mental foramen below:  $P_1$ - $P_2$  indicates very probably *Canis*,  $P_2$  indicates very probably *Cuon alpinus* and  $P_2$  anterior indicates nothing.

The posterior foramen does not occur below  $P_2$ - $P_3$  in *Cuon alpinus*. The 'peak occurrence' of the foramen lies at  $P_3$  posterior and percentages decline rapidly towards more anterior positions of the posterior foramen. Based on this dataset it is thus very unlikely that a specimen with a posterior foramen below  $P_2$ - $P_3$  is *Cuon alpinus*. The posterior foramen does occur below  $P_2$ - $P_3$  in *C. l. familiaris*, but not in *C. l. lupus*, which is peculiar, since both species have similar results for the rest of the positions: both species have their 'peak occurrence' below  $P_3$  anterior (with about 50%), after which percentages decline again. A sudden jump in *C. l. lupus* from zero occurrences below  $P_2$ - $P_3$  to 50% occurrence below  $P_3$  anterior is quite large and it is likely that a posterior foramen below  $P_2$ - $P_3$  also is possible in *C. l. lupus*, but that this is not observed in this comparative dataset, because the *C. l. lupus* dataset is much smaller than that of *C. l. familiaris*. Based on position  $P_2$ - $P_3$  *C. l. lupus* can thus not be excluded as possibility.  $P_3$  anterior is a very common place for the posterior foramen in both *Canis* species, but quite rare in *Cuon alpinus*. When this position is encountered in a fossil specimen, the chance is thus much higher that this specimen belongs to either two of the *Canis* species, although *Cuon alpinus* cannot entirely be excluded as possibility. The posterior mental foramen occurs below  $P_3$  in a significant number of specimens in all three comparative species, thus nothing can be concluded about the identity of a specimen in which this position of the posterior foramen is encountered. The 'peak occurrence' of the posterior foramen in *Cuon alpinus* is below  $P_3$  posterior and this position is encountered much less frequently in *Canis*. The chance is thus much higher that, when this position is encountered in a fossil specimen, the specimen belongs *Cuon alpinus*, although both *Canis* cannot entirely

be excluded as possibility. The posterior foramen is only encountered below  $P_4$  in *Cuon alpinus* and, since occurrences of this foramen in *Canis* already show a declining trend from  $P_3$  anterior towards more posterior positions, it is very likely that a specimen with a posterior foramen below  $P_4$  is *Cuon alpinus*. This is an example of extreme distal displacement of the posterior foramen in *Cuon alpinus*. Summarized, the position of the posterior mental foramen below:  $P_2$ - $P_3$  indicates very probably *Canis*,  $P_3$  anterior indicates more likely *Canis*,  $P_3$  indicates nothing,  $P_3$  posterior indicates more likely *Cuon alpinus* and  $P_4$  indicates very probably *Cuon alpinus*.

Absence of mental foramina in a specimen does not give any indication about the identity of that specimen, since it is the *position* of the foramina, if present, that gives an indication about what species a specimen might be and not the *number* or appearance of foramina that are present.

#### **5.2.4.2 Fossil North Sea material**

All results that are discussed in this paragraph can be found in 4.1.5.2.

##### **Specimens 534, 535 and NMR90**

These three specimens miss a large (anterior) part of the hemimandible, thus the position of the middle and posterior mental foramina could not be established.

##### **Specimens 667, 1683, 2104, 2329 and 3293**

In these five specimens the middle mental foramen is positioned below  $P_1$ - $P_2$ , which means that these specimens are very probably *Canis* specimens and do not belong to *Cuon alpinus*. Which of the two *Canis* specimens they are cannot be determined from this parameter.

In specimen 667 and 2329 the posterior foramen is positioned below  $P_2$ - $P_3$ , which confirms the conclusion that these two specimens are very probably *Canis* specimens. In specimen 2104 and 3293 the posterior foramen is positioned below  $P_3$  anterior, which is not as strong an indication for their *Canis* identity as the position of the middle foramen (since it does not exclude *Cuon alpinus* as a possibility), but it still confirms the conclusion for these specimens that was based on the middle foramen. In specimen 1683 the posterior foramen is positioned below  $P_3$  posterior, which is more typical for *Cuon alpinus* than for *Canis*. This means that this specimen likely would be *Cuon alpinus*, although the possibility that this specimen is *Canis* cannot be excluded with this parameter. When one compares the conclusions from the middle and posterior mental foramen for this specimen, we can conclude that based on the parameter 'Mental foramina' 1683 is more likely to be a *Canis* specimen, because the conclusion from the middle foramen is slightly more conclusive than the conclusion based on the posterior foramen.

##### **Specimens 2103, 2196, 2620, 3219 and NMR89**

In these five specimens the middle mental foramen is positioned below  $P_2$  anterior, which does not indicate to which species these specimens belong, since the middle mental foramen occurs below  $P_2$  anterior in similar percentages for all three comparative species.

Specimen 2103 does not have a posterior mental foramen and specimen 2196, 3219 and NMR89 have their posterior foramen at position  $P_3$ , thus based on the mental foramina nothing can be concluded about the identity of these specimens. The posterior foramen is located below  $P_3$  posterior in specimen 2620, which means that this specimen likely is *Cuon alpinus*, although the possibility that this specimen is *Canis* cannot be excluded with this parameter. Based on the mental foramina nothing conclusive can thus be stated about the identity of these fossil North Sea specimens.

#### **5.2.5 Incisors**

In almost all comparative *Cuon alpinus* specimens the lower incisor alveoli form an equilateral triangle due to crowding of the incisors and in almost all *C. l. lupus* specimens the incisors are positioned in a row (4.1.6). In *C. l. familiaris* incisors are also positioned in a row in most specimens, although crowdedness also occurs. When a fossil specimen has its incisors placed in a row, we can conclude that the mandible was large enough to contain all teeth and there is a much greater chance that this specimen belongs to the genus *Canis* (either *C. l. familiaris* or *C. l. lupus*, that difference cannot be made based on this parameter). On the other hand, when a specimen has crowded incisors, this means that the mandible was quite small and the specimen probably belongs to *Cuon alpinus*. But in both cases *Cuon alpinus* respectively *Canis* cannot be entirely excluded as possibility, because, although rarely, crowded incisors respectively incisors placed in a row can occur in *Canis* respectively *Cuon alpinus*. The fact that in *C. l. familiaris* crowdedness of incisors occurs more often than in *C. l. lupus* can be explained by the larger sample size of *C. l. familiaris* that includes relatively small mandibles that are of similar size as *Cuon alpinus* mandibles, while *C. l. lupus* in general has larger mandibles and does not reach the (smaller) *Cuon alpinus* values (5.2.1.1).

### Specimen 2104, 2620 and 3219

Only for these three specimens the position of the incisors could be determined: the incisor alveoli are positioned nicely in a row. This means that these specimens are probably *Canis* specimens, although it cannot be excluded that they are *Cuon alpinus*. This parameter cannot give any conclusive evidence for the identity of these fossil North Sea specimens; it only provides an indication and thereby confirms conclusions obtained by previous parameters.

## 5.2.6 Conclusions section 'Mandible length'

In this paragraph (preliminary) conclusions about the identity of the 13 fossil North Sea specimens will be drawn, based on the combined conclusions of the individual parameters that were presented in this first 'Mandible length' section. For an overview of all results and interpretation thereof, see appendix XII.

### Specimen 534 (*C. l. lupus*)

Specimen 534 could only be measured for 2 out of 10 subparameters of the 'Mandible length' section ('Length of the mandible' *a-b* and *c-b*, table XII.1) and these two parameters even had to be estimated with a comparative *C. l. lupus* specimen. Although these values are estimates the evidence for a *C. l. lupus* identity of specimen 534 is very strong: the specimen range of 534 fell far above the *C. l. familiaris* and *Cuon alpinus* ranges, thus even if the actual values of 534 for these subparameters would have been slightly different, this specimen would still be too large to be either *C. l. familiaris* or *Cuon alpinus*. Qualitative comparison of specimen 534 with all comparative material also already indicated that 534 is a quite large mandible part and is larger in size than all comparative *C. l. familiaris* and *Cuon alpinus* specimens. According to all combined evidence of the 'Mandible length' section specimen 534 can be assigned to *C. l. lupus* with a 97.7% confidence interval.

### Specimen 535 (*C. l. lupus*)

Specimen 535 could only be measured for 3 out of 10 subparameters of the 'Mandible length' section ('Length of the mandible' *a-b* and *c-b* and 'Alveolar length'  $M_1-M_2$ , table XII.1). Values of subparameters *a-b* and *c-b* had to be estimated based on a comparative *C. l. lupus* specimen, but could only identify specimen 535 on genus level (535 is *Canis* and not *Cuon alpinus*, 97.7% confidence interval). Based on the alveolar length  $M_1-M_2$  specimen 535 could be identified as a *C. l. lupus* specimen with a 97.7% confidence interval, because the specimen range of 535 fell far above the *C. l. familiaris* and *Cuon alpinus* ranges. The conclusion that 535 is not *Cuon alpinus* was extra confirmed by the new statistics based on an extended dataset that included 6 *Cuon alpinus* specimens from literature. According to the three parameters of the 'Mandible length' section specimen 535 can be assigned to *C. l. lupus* with a 97.7% confidence interval.

### Specimen 667 (*C. l. familiaris*)

Specimen 667 was measured for all parameters of the 'Mandible length' section, except the incisors (table XII.2). The parameter 'Diastema length' between  $P_2-P_3$  and  $P_3-P_4$  was entirely inconclusive, but all other parameters in this section did give indications for the identity of specimen 667. When all conclusions are combined we see that a *C. l. lupus* identity is excluded by all five (quantitative) subparameters of 'Mandible length' and 'Alveolar length', thus the chance that specimen 667 is *C. l. lupus* is even smaller than 2.3% (as explained in 2.2.4). A *Cuon alpinus* identity is also excluded by five (sub)parameters: lengths of the mandible *a-b* and *c-b*, 'Diastema length'  $C-P_1$  and the two mental foramina. The confidence level of this conclusion is not increased to larger than 97.7% (as was the case for *C. l. lupus*), because not all five parameters are quantitative and because the values for the mandible length were not the actual values of this specimen, but estimates based on a comparative *C. l. familiaris* specimen. The possibility that specimen 667 is *C. l. familiaris* is confirmed by all 9 parameters of this section. Additionally, qualitative evidence indicated that 667 is indeed smaller than all comparative *C. l. lupus* material and less sturdy than *Cuon alpinus* specimens. Based on the combined evidence of all parameters in the 'Mandible length' section specimen 667 can be assigned to *C. l. lupus* with a 97.7% confidence interval.

### Specimen 1683 (*C. l. lupus*)

Specimen 1683 was also measured for all parameters of the 'Mandible length' section, except the incisors (table XII.2). The possibility of a *Cuon alpinus* identity for specimen 1683 was excluded by all parameters except the posterior mental foramen. Six of these parameters were quantitative, which means that the chance that specimen 1683 is *Cuon alpinus* is even smaller than 2.3%. The conclusion that 1683 is not *Cuon alpinus* was extra confirmed by the new statistics based on the extended dataset of parameters 'Alveolar length'  $P_1-M_2$  and  $M_1-M_2$  that included 6 *Cuon alpinus* specimens from literature. *C. l. familiaris* was excluded as possible identity for 1683 by six quantitative parameters (all mandible lengths, all alveolar lengths and diastema length  $C-P_1$ ) and one qualitative parameter (posterior foramen), which means that the chance that specimen 1683 is *C. l. familiaris* is also smaller than 2.3%. Although the values of *a-b* and *c-b* are estimates

based on a *C. l. lupus* specimen the evidence for a *C. l. lupus* identity of specimen 1683 is very strong: the specimen range fell far above the *C. l. familiaris* and *Cuon alpinus* ranges, thus even if the actual values of 1683 for these subparameters would have been slightly different, this specimen would still be too large to be either *C. l. familiaris* or *Cuon alpinus*. The possibility that specimen 1683 is *C. l. lupus* is confirmed by all parameters in this section, except the posterior foramen. This is the only parameter that points towards a *Cuon alpinus* identity, but the evidence of all other parameters is much stronger (statistically). Moreover, qualitative evidence also indicates that 1683 is very probably a *C. l. lupus* specimen: this specimen was larger than all comparative *C. l. familiaris* and *Cuon alpinus* material with respect to its mandible length and was even more heavily built, with a greater width and height of the mandible than the largest comparative *C. l. lupus* specimen. We can conclude based on the combined evidence of all parameters in the 'Mandible length' section that specimen 1683 can be assigned to *C. l. lupus* with a 97.7% confidence interval.

#### **Specimen 2103 (*C. l. familiaris*)**

Specimen 2103 was measured for 8 of the 10 subparameters of the 'Mandible length' section (table XII.3). The middle mental foramen was entirely inconclusive, but all other 7 subparameters in this section did give indications for the identity of this fossil North Sea specimen. The possibility that specimen 2103 is a *C. l. familiaris* specimen was confirmed by all 7 subparameters. A *Cuon alpinus* identity was initially excluded by 6 quantitative parameters ('Length of the mandible' *a-b* and *c-b*, all three alveolar lengths and 'Diastema length' C-P<sub>1</sub>) and 1 qualitative parameter ('Diastema length' P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub>), but the values of the two mandible lengths were estimates based on a comparative *C. l. familiaris* specimen and based on the extended dataset of alveolar lengths P<sub>1</sub>-M<sub>2</sub> and M<sub>1</sub>-M<sub>2</sub>, which included 6 additional *Cuon alpinus* values from literature, specimen 2103 falls within the *Cuon alpinus* population ranges. This means that parameters 'Alveolar length' P<sub>1</sub>-M<sub>2</sub> and M<sub>1</sub>-M<sub>2</sub> do not exclude *Cuon alpinus* as possibility after all and that the conclusions based on the mandible lengths are slightly less conclusive than those for 'Alveolar length' P<sub>4</sub>-M<sub>1</sub>-M<sub>2</sub> and 'Diastema length' C-P<sub>1</sub>. But then still 4 quantitative subparameters ('Length of the mandible' *a-b* and *c-b* (although slightly less conclusive), 'Alveolar length' P<sub>4</sub>-M<sub>1</sub>-M<sub>2</sub> and 'Diastema length' C-P<sub>1</sub>) and 1 qualitative parameter ('Diastema length' P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub>) remain, that indicate that specimen 2103 is not *Cuon alpinus*, which means that the chance that 2103 is *Cuon alpinus* is less than 2.3%. A *C. l. lupus* identity for specimen 2103 was only excluded by 2 quantitative subparameters ('Alveolar length' P<sub>4</sub>-M<sub>1</sub>-M<sub>2</sub> and M<sub>1</sub>-M<sub>2</sub>). Qualitative evidence confirms a *C. l. familiaris* identity for specimen 2103: this fossil specimen appeared bigger than all *Cuon alpinus* comparative material and qua overall appearance it did not compare well to *C. l. lupus*, because the specimen is more fragile (like *C. l. familiaris*) and is also smaller than most comparative *C. l. lupus* specimens. Based on the combined evidence of all parameters in the 'Mandible length' section and with a 97.7% confidence interval we can conclude that specimen 2103 belongs to the subspecies *C. l. familiaris*.

#### **Specimen 2104 (*C. l. familiaris*)**

This fossil North Sea specimen was measured for all 10 subparameters of the 'Mandible length' section (table XII.3). Parameters 'Length of the mandible' *c-b*, 'Alveolar length' P<sub>1</sub>-M<sub>2</sub>, all diastema lengths, both mental foramina and the incisors indicated that specimen 2104 is not *Cuon alpinus*. For parameter 'Alveolar length P<sub>1</sub>-M<sub>2</sub>' this conclusion was later invalidated, because specimen 2104 did fall within the *Cuon alpinus* population range of this parameter for the new extended dataset (that includes 6 *Cuon alpinus* values from literature). This means that two quantitative parameters remain based on which we can conclude that the chance that 2104 is *Cuon alpinus* is only 2.3% (the qualitative parameters do not give a statistical confidence interval). Four quantitative parameters ('Length of the mandible' *a-b* and *c-b* and 'Alveolar lengths' P<sub>4</sub>-M<sub>1</sub>-M<sub>2</sub> and M<sub>1</sub>-M<sub>2</sub>) indicated that specimen 2104 is not *C. l. lupus* (thus the chance that 2104 is *C. l. lupus* is even smaller than 2.3%). All parameters indicated that it is possible that specimen 2104 is *C. l. familiaris*: there are no 'problems' (red characters in table XII.3 indicating partial or no overlaps) for this subspecies. Based on the combined evidence of all parameters in the 'Mandible length' section and with a 97.7% confidence interval we can conclude that specimen 2104 belongs to the subspecies *C. l. familiaris*.

#### **Specimen 2196 (*C. l. lupus*)**

Specimen 2196 was measured for all 10 subparameters of the 'Mandible length' section, except the incisors (table XII.4). The mental foramina were inconclusive about the identity of this fossil North Sea specimen and the diastema lengths C-P<sub>1</sub>, P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub> only gave an indication on genus level (2196 is *Canis* and not *Cuon*). The remaining 5 subparameters were very conclusive and excluded both *C. l. familiaris* and *Cuon alpinus* as possible identity for specimen 2196. The values for the mandible lengths were estimated based on a *C. l. lupus* specimen and are thus actually slightly less conclusive, but they also indicated that 2196 is even quite large for a *C. l. lupus* specimen (the specimen range of 2196 fell partially above the *C. l. lupus* population ranges), which cancels out the fact that the conclusions based on these parameters should be regarded as slightly less conclusive as explained for previous specimens (534). The results of the extended dataset (including 6 *Cuon alpinus* values from literature) for parameters 'Alveolar length' P<sub>1</sub>-M<sub>2</sub> and M<sub>1</sub>-M<sub>2</sub>) confirmed the results obtained by the original dataset. Qualitative evidence confirms the conclusion that



2196 is *C. l. lupus*: specimen 2196 was larger than all comparative *C. l. familiaris* and *Cuon alpinus* material and is much robust than a *Cuon alpinus* or *C. l. familiaris* specimen. Based on the combined evidence of all parameters in the 'Mandible length' section and with a 97.7% confidence interval we can conclude that specimen 2196 is a *C. l. lupus* specimen.

#### **Specimen 2329 (*C. l. lupus*)**

This specimen was also measured for all 10 subparameters of the 'Mandible length' section, except the incisors (table XII.4). All diastema lengths and the mental foramina only gave an indication for the identity of specimen 2329 on genus level (2329 is not *Cuon*, but *Canis*). All quantitative parameters were very conclusive and indicated that there is only a 2.3% chance that 2329 is *Cuon alpinus* (6 quantitative parameters) or *C. l. familiaris* (5 quantitative parameters). This chance is even slightly smaller than 2.3%, because there are multiple parameters excluding these (sub)species. The values for the mandible lengths were estimated based on a *C. l. lupus* specimen and are thus actually slightly less conclusive, but on the other hand they indicated that 2196 is even quite large for a *C. l. lupus* specimen and it is thus very likely that the actual mandible lengths of 2329 also would have fallen far above the *C. l. familiaris* and *Cuon alpinus* ranges. Moreover, the results of the extended dataset (including the *Cuon alpinus* values from literature) for parameters 'Alveolar length' P<sub>1</sub>-M<sub>2</sub> and M<sub>1</sub>-M<sub>2</sub>) confirmed the results obtained by the original dataset. We can conclude based on the combined evidence of all parameters in the 'Mandible length' section that specimen 2329 can be assigned to *C. l. lupus* with a 97.7% confidence interval.

#### **Specimen 2620 (*C. l. lupus*)**

Specimen 2620 was measured for all 10 subparameters of the 'Mandible length' section (table XII.5). The middle mental foramen was inconclusive about the identity of fossil specimen 2620. Diastema lengths P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub> and the incisors indicated that 2620 is more likely *Canis* than *Cuon*, but the posterior foramen indicated that this fossil specimen more likely is *Cuon* than *Canis*. These parameters were thus not very conclusive and, moreover, contradictory. Fortunately, the remaining 6 quantitative (sub)parameters (mandible lengths, alveolar lengths and 'Diastema length' C-P<sub>1</sub>) were more conclusive: 'Diastema length' C-P<sub>1</sub> indicated that 2620 is not *Cuon* but *Canis* and the other 5 parameters all 'conclusively' (97.7% confidence interval) indicated that specimen 2620 is *C. l. lupus*. For some of these 5 parameters the specimen range even fell (partially) above the *C. l. lupus* ranges, confirming that 2620 is too large to be *C. l. familiaris* or *Cuon alpinus* and indicating that the specimen is even quite large for a *C. l. lupus* specimen (canceling out the fact that conclusions based on the mandible lengths should be less conclusive, because they were estimated). Additional evidence for the assignment of 2620 to *C. l. lupus* comes from the qualitative comparison of 2620 with the comparative material: specimen 2620 appears to be slightly more heavily built than the largest comparative *C. l. lupus* specimen. The conclusion that 2620 is not *Cuon alpinus* was confirmed by the extended dataset (including values from literature). We can thus conclude based on the combined evidence of all parameters in the 'Mandible length' section that specimen 2620 can be assigned to *C. l. lupus* with a 97.7% confidence interval.

#### **Specimen 3219 (*Canis*)**

Specimen 3219 was measured for all 10 subparameters of the 'Mandible length' section (table XII.5). Both mental foramina were inconclusive about the identity of specimen 3219 and the remaining two qualitative parameters (incisors and diastema lengths P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub>) only identified 3219 on genus level: 3219 is *Canis* and not *Cuon*. The remaining 6 quantitative parameters were neither entirely conclusive about the identity of fossil specimen 3219: based on parameter 'Alveolar length' P<sub>1</sub>-M<sub>2</sub> specimen 3219 could be one of all comparative (sub)species (taking into account the results of the extended dataset that includes *Cuon alpinus* values from literature that indicated, on the contrary to the original dataset, that it is possible that 3219 is *Cuon alpinus*). The other 5 parameters ('Length of the mandible' a-b and c-b, 'Alveolar length' P<sub>4</sub>-M<sub>1</sub>-M<sub>2</sub> and M<sub>1</sub>-M<sub>2</sub> and 'Diastema length' C-P<sub>1</sub>) could only identify 3219 as a *Canis* specimen. Qualitative comparison of 3219 with *C. l. familiaris* and *C. l. lupus* material indicated that 3219 does not compare well to *C. l. lupus* qua overall appearance (it looks more fragile like *C. l. familiaris*), but 'looking more like' is not very solid evidence based on which conclusive statements can be made. Based on the combined evidence of all parameters in the 'Mandible length' section we can only identify specimen 3219 on genus level - assign it to *Canis* - with a 97.7% confidence interval.

#### **Specimen 3293 (*C. l. lupus*)**

This fossil North Sea specimen was measured for all 10 subparameters of the 'Mandible length' section, except the incisors (table XII.6). Both mental foramina and 'Diastema length' P<sub>2</sub>-P<sub>3</sub> and P<sub>3</sub>-P<sub>4</sub> only identified specimen 3293 on genus level: 3293 is more likely *Canis* than *Cuon*. Results based on the new statistics of the extended dataset (that includes *Cuon alpinus* values from articles) of parameters ('Alveolar length' P<sub>1</sub>-M<sub>2</sub> and M<sub>1</sub>-M<sub>2</sub>) confirmed that 3293 is too large to be *Cuon alpinus* with a 97.7% confidence interval. Based on all other 6 parameters and the qualitative description of this hemimandible (3293 is a large, thick and robust hemimandible, unlike *C. l. familiaris* and larger than all comparative *C. l. familiaris* and *Cuon alpinus*

material) specimen 3293 could be identified as a *C. l. lupus* specimen with a 97.7% confidence interval (*Cuon alpinus* was excluded by 6 quantitative subparameters and *C. l. familiaris* was excluded by 5 quantitative parameters).

**Specimen NMR89 (*C. l. lupus*)**

NMR89 was measured for 8 of the 10 subparameters of the 'Mandible length' section (table XII.6). Both mental foramina were entirely inconclusive about the identity of NMR89 and the diastema lengths  $P_2-P_3$  and  $P_3-P_4$  and mandible lengths  $a-b$  and  $c-b$  could only identify NMR89 as belonging to the genus *Canis*. The qualitative description of NMR89 confirmed that NMR89 is larger than all comparative *Cuon alpinus* specimens, but qualitatively it is hard to tell whether this hemimandible is more similar to *C. l. lupus* or *C. l. familiaris*. All three alveolar lengths on the other hand conclusively (97.7% confidence interval) indicated that NMR89 is *C. l. lupus*. The conclusion that NMR89 is not *Cuon alpinus* was confirmed by the extended dataset that includes *Cuon alpinus* values from literature for alveolar lengths  $P_1-M_2$  and  $M_1-M_2$ .

**Specimen NMR90 (*C. l. familiaris*)**

Specimen NMR90 could only be measured for 4 out of 10 subparameters of the 'Mandible length' section ('Length of the mandible'  $a-b$  and  $c-b$  and 'Alveolar length'  $P_4-M_1-M_2$  and  $M_1-M_2$ ) (table XII.7). *Cuon alpinus* was excluded as possible identity for NMR90 based on 3 quantitative subparameters (mandible lengths  $a-b$  and  $c-b$  and alveolar length  $P_4-M_1-M_2$ ), although we have to keep in mind that the values for the mandible length were not the actual values of NMR90, but estimates based on a comparative *C. l. familiaris* specimen. But since the results of the mandible lengths are confirmed by the results of the alveolar lengths (which are not estimated) we can reasonably assume that the results of the mandible lengths are valid. *C. l. lupus* was excluded as possible identity for NMR90 based on 2 quantitative subparameters ('Mandible length'  $a-b$  and 'Alveolar length'  $P_4-M_1-M_2$ ). All parameters left open the possibility that NMR90 is *C. l. familiaris*: as can be seen in table XII.7, where there are 'problems' (partial overlaps, NMR90 falls outside the ranges) for NMR90 in the *Cuon alpinus* and *C. l. lupus* categories, there are none for *C. l. familiaris*. Qualitative evidence (overall appearance of the mandible: mandible ratios, size, length, robustness) indicated that specimen NMR90 is completely unlike typical *Cuon alpinus* or *C. l. lupus* mandibles, because it has other mandible ratios than *Cuon alpinus* and is smaller and less robust than *C. l. lupus*, while NMR90 coincides very well with *C. l. familiaris* specimens on all these points. Based on the combined evidence of all parameters in the section 'Mandible length' and with a confidence of 97.7% we can conclude that specimen NMR90 is not a *C. l. lupus* specimen, not a *Cuon alpinus* specimen, but a *C. l. familiaris* specimen.

## 5.3 Mandible (width, height and ratios)

### 5.3.1 Mandible width $i-i'$ and $k-k'$

Since parameters  $i-i'$  and  $k-k'$  have similar results (4.2.1), they will be interpreted together and, if is not explicitly stated otherwise, in each paragraph conclusions hold true for both parameters. Only where parameters  $i-i'$  and  $k-k'$  do not have the same results, results will be mentioned separately.

#### 5.3.1.1 Comparative material

Results of the comparative material for these two parameters are as expected and there are no remarkable observations, except that mandible width is more variable than anteriorly thought (higher amount of overlap between the three comparative species, 4.2.1.1). All (general) explanations and statements about the interpretation of means, sample and population ranges and distinction between fossil specimens from the Netherlands and recent specimens from Suriname that could be made about these results are already mentioned in the paragraphs of previous parameters and also hold true for these parameters (see previous paragraphs and mainly 5.2.1.1).

#### 5.3.1.2 Fossil North Sea material

All results that are discussed in this paragraph can be found in 4.2.1.2.

#### Specimen 535

Specimen 535 lacks values for parameter  $k-k'$ , thus following statements only refer to  $i-i'$ . This specimen is small compared to *C. l. lupus* specimens and large compared to *Cuon alpinus*, but it falls entirely within all sample and population ranges of all comparative material for this parameter. This means that based on this parameter it cannot be determined which of the three comparative species 535 is. The position of 535 compared to the mean values of the comparative species, which indicates that 535 is most similar to the average *C. l. familiaris* specimen and less similar to the average *Cuon alpinus* and *C. l. lupus* specimens, is of no value, because there are no previous conclusions to support or oppose. Specimen 535 can be *Canis* or *Cuon alpinus*.

#### Specimen 667

Also specimen 667 cannot be assigned to one of the three comparative species for this parameter, because the specimen range of 667 falls entirely within all sample and population ranges of all comparative species. The fact that 667 partly falls outside (above) the population range of *Cuon alpinus* for parameter  $k-k'$ , does not significantly reduce the chance that 667 is *Cuon alpinus*. Also the circumstantial indication for the identity of 667 (667 is most similar to the average *C. l. familiaris* specimen) is of no significant value as explained above. Thus specimen 667 also can be *Canis* or *Cuon*.

#### Specimen 1683

Specimen 1683 falls entirely outside (above) the sample and population ranges of *Cuon alpinus* for both parameters, which means that there is only a 2.3% chance that 1683 is *Cuon alpinus*. Based on parameter  $k-k'$  *C. l. familiaris* cannot be excluded, because 1683 falls entirely within the *C. l. familiaris* sample range and for most part within the population range. This partial overlap instead of entire overlap does not significantly reduce the chance that 1683 is *C. l. familiaris*. Based on parameter  $i-i'$ , however, can be concluded that specimen 1683 is very probably not *C. l. familiaris*, because 1683 falls entirely outside (above) the sample and population range of *C. l. familiaris* for this parameter, which means that there is only a 2.3% chance that 1683 is *C. l. familiaris*. From the sample and population ranges of these parameters can thus be concluded that specimen 1683 is almost certainly a *C. l. lupus* specimen (1683 falls within the sample and population ranges of *C. l. lupus* for both parameters). Circumstantial evidence (the mean value of specimen 1683 is most similar to the average *C. l. lupus* specimen) confirms this conclusion.

#### Specimen 2103

Results of specimen 2103 are not very conclusive. The specimen range of 2103 falls entirely outside (below) the *C. l. lupus* sample range ( $i-i'$ ), which is an initial indication that 2103 might not be *C. l. lupus*, but there is a very slight overlap (0.02 mm) of the 2103 specimen range with the *C. l. lupus* population range ( $i-i'$ ). This means that there is still a chance that 2103 is *C. l. lupus*, thus *C. l. lupus* cannot entirely be excluded as possibility for the identity of specimen 2103. For parameter  $k-k'$  specimen 2103 falls entirely inside the *Cuon alpinus* sample range and for most part inside the *Cuon alpinus* population range, which means that the chance that 2103 is *Cuon alpinus* is not significantly reduced, thus *Cuon alpinus* neither can be excluded. Specimen 2103 falls within all remaining sample and population ranges. Based on the sample and population ranges we can conclude that specimen 2103 is not likely a *C. l. lupus* specimen, but the likelihood cannot be expressed in percentages, because this conclusion is only based on the sample range. The mean

value of 2103 lies closer to the mean *Cuon alpinus* for *i-i'*, but closer to the mean *C. l. familiaris* for *k-k'*. For both parameters 2103 is most dissimilar to *C. l. lupus*. This confirms the conclusion already obtained by the ranges: specimen 2103 is possibly not *C. l. lupus* and it cannot be concluded whether 2103 is *C. l. familiaris* or *Cuon alpinus*.

#### **Specimen 2104**

Based on mandible width cannot be determined which of the three comparative species specimen 2104 is, because the specimen range of 2104 falls within the sample and population ranges of all comparative species for both parameters. The mean of 2104 compared to the mean values of the comparative species, which indicates that 2104 is most similar to the average *C. l. familiaris* specimen, is of no value, because there are no previous conclusions to support or oppose. Specimen 2104 can be *Canis* or *Cuon*.

#### **Specimen 2196**

Results indicate that this specimen is almost certainly a *C. l. lupus* specimen. Specimen 2196 already falls for most part of its range outside (above) the *C. l. familiaris* sample range for *k-k'* and also entirely outside all other sample and population ranges for *Cuon alpinus* and *C. l. familiaris* for both parameters. Based on the population ranges we can conclude that there is only a 2.3% chance that 2196 is *Cuon alpinus* or *C. l. familiaris*. This specimen has a quite wide mandible for a *C. l. lupus*, because 2196 even falls slightly above the *C. l. lupus* population range for parameter *k-k'* (this does not reduce the chance that 2196 is *C. l. lupus*). Circumstantial evidence (the mean value of 2196 is most similar to the average *C. l. lupus* specimen) supports the conclusion that 2196 is a *C. l. lupus* specimen.

#### **Specimen 2329**

Based on mandible width can be concluded that specimen 2329 is a *C. l. familiaris* or *C. l. lupus* specimen. The sample range of parameter *i-i'* indicates that 2329 still could be *Cuon alpinus*, but the sample range of *k-k'* and the *Cuon alpinus* population ranges for both parameters exclude this possibility, because the mandible of specimen 2329 is too wide to fit within these ranges. 97.7% Of all *Cuon alpinus* specimens have a mandible that is smaller than that of specimen 2329, thus 2329 is almost certainly not *Cuon alpinus*. Mean values indicate that specimen 2329 is most similar to the average *C. l. lupus* specimen and least similar to the average *Cuon alpinus* specimen, which confirms the conclusion that 2329 is not *Cuon alpinus*, but does not conclusively prove that 2329 is *C. l. lupus*. Specimen 2329 can be either of the two *Canis* species, based on its mandible width.

#### **Specimen 2620**

Specimen 2620 falls entirely outside (above) the *Cuon alpinus* sample and population ranges for both parameters, which means that 2620 is almost certainly not a *Cuon alpinus* specimen, because the chance of that is only 2.3% (although there is still a small possibility that 2620 is a *Cuon alpinus* specimen with extremely wide mandibles). Specimen 2620 falls for most part inside the *C. l. familiaris* sample range and for most part outside (above) the *C. l. familiaris* population range for parameter *k-k'*, but these partial overlaps do not significantly reduce the chance that 2620 is *C. l. familiaris*. Solely based on mandible width this species can thus not be excluded as possible identity for hemimandible 2620. The specimen range of 2620 falls entirely within the sample and population ranges of *C. l. lupus* for both parameters and could thus very well be this species. Mean values indicate that 2620 is most similar to the average *C. l. lupus* specimen, but this is just an indication. Specimen 2620 can be either of both *Canis* species.

#### **Specimen 3219**

Results of specimen 3219 are very clear: the specimen range of 3219 falls entirely within the sample and population ranges of all comparative material for both parameters, except in the *Cuon alpinus* sample and population ranges for parameter *k-k'*. This means that 97.7% of the natural *Cuon alpinus* population has smaller mandibles than specimen 3219 and that the chance that this specimen is *Cuon alpinus* is very small. Specimen 3219 is very likely a *Canis* specimen. Results of the mean values for this specimen indicate well how circumstantial evidence from mean values is: the mean value of specimen 3219 for parameter *i-i'* is most similar to the average *C. l. familiaris* specimen and most dissimilar to the average *C. l. lupus* specimen, but for parameter *k-k'* 3219 is most similar to the average *C. l. lupus* specimen and most dissimilar to the average *Cuon alpinus*. Although these comparisons indicate that 3219 indeed is more similar to *Canis* than to *Cuon alpinus* it also shows how variable the outcomes can be.

Following three specimens do not have values for parameter *k-k'*, thus statements only refer to *i-i'*.

#### **Specimen 3293**

Specimen 3293 is almost certainly not *Cuon alpinus*, because it falls entirely outside (above) the *Cuon alpinus* sample and population ranges; there is only a 2.3% chance that 3293 is *Cuon alpinus*. Specimen 3293 is thus a *Canis* specimen, but based on mandible width cannot be determined which of the two

species, because 3293 falls entirely within the sample and population ranges of *C. l. lupus* and for most part within the *C. l. familiaris* sample and population ranges. There is an equal chance that 3293 is *C. l. lupus* or *C. l. familiaris*. Mean values indicate that specimen 3293 is more similar to the average *C. l. lupus* specimen than to the average *C. l. familiaris*, but this is far from conclusive.

#### **Specimen NMR89**

Based on results for mandible width no conclusion can be drawn about the identity of this specimen: NMR89 falls within the sample and population ranges of all comparative material. Overlap is partial for the *Cuon alpinus* population range, but this does not reduce the chance that NMR89 is *Cuon alpinus*. The mean value of NMR89 is most similar to the average *C. l. familiaris* specimen, but solely based on this slight indication no conclusion can be drawn: NMR89 can be either *Canis* or *Cuon* based on its mandible width.

#### **Specimen NMR90**

Also for this specimen evidence is not conclusive: NMR90 falls entirely in all sample and population ranges of all three comparative species and can thus be either *Cuon* or *Canis* based on its mandible width. Solely based on circumstantial evidence (the mean value of NMR90 is most similar to the average *C. l. familiaris* specimen) NMR90 cannot be identified.

### **5.3.2 Mandible height $h-h'$**

Since all mandibular heights have similar results (4.2.2.1, 4.2.3.1 and 4.2.4.1),  $P_1$  and  $P_2$ ,  $P_3$  and  $P_4$ , and  $M_1$  and  $M_2$  will be interpreted together: if is not explicitly stated otherwise in each paragraph conclusions hold true for both parameters. Only where the parameters do not have the same results, results will be mentioned separately. Results of the North Sea specimens for parameters  $P_3$ ,  $P_4$ ,  $M_1$  and  $M_2$  are discussed briefly, to prevent unnecessary repetition of statements that were already made in the discussion of the results of  $P_1$  and  $P_2$ . Everything that could be interpreted about the comparative material was already done for previous parameters (see previous paragraphs and mainly 5.2.1.1). Results of the comparative material for these six parameters are as expected (thus similar to previous parameters): there are no remarkable observations. No particular interpretations are made for these parameters.

#### **5.3.2.1 Mandible height $h-h'$ under $P_1$ and $P_2$ (Fossil North Sea material)**

All results that are discussed in this paragraph can be found in 4.2.2.2.

#### **Specimen 667**

Specimen 667 is probably not a *C. l. lupus* specimen. The specimen range of 667 slightly overlapped with the lower part of the *C. l. lupus* population range for  $h-h'$   $P_1$ , which means that based on this specific range of this parameter 667 still could be *C. l. lupus*. But specimen 667 fell entirely outside (below) the remaining sample and population ranges of *C. l. lupus*, based on which we can conclude that there is only a 2.3% chance that specimen 667 is *C. l. lupus*. Mean values and trend lines circumstantially confirmed this: the mean value of 667 is most dissimilar to the average *C. l. lupus* specimen and plots relatively far away from the *C. l. lupus* data cloud, close to the *C. l. familiaris* and *Cuon alpinus* trend lines. From these two mandible heights we cannot conclude whether 667 is *Cuon alpinus* or *C. l. familiaris*, because this specimen falls entirely within the sample and population ranges of both these species. The mean values and trend lines neither give any indication for the identity of specimen 667, because the mean of 667 is most similar to *Cuon alpinus* for one parameter and to *C. l. familiaris* for the other parameter and plots in the middle of the data clouds of both species in fig. 4.14. Specimen 667 is thus either *Cuon alpinus* or *C. l. familiaris*, but almost certainly not *C. l. lupus*.

#### **Specimen 1683**

Based on these two mandible heights 1683 is a *C. l. lupus* specimen. Specimen 1683 falls entirely outside (above) the sample and population ranges of *Cuon alpinus* and *C. l. familiaris* and entirely within the sample and population ranges of *C. l. lupus*, which means that there is only a 2.3% chance that 1683 is *Cuon alpinus* or *C. l. familiaris*. Circumstantial evidence supports the conclusion that 1683 is *C. l. lupus*: the mean value of 1683 is most similar to the average *C. l. lupus* specimen and much more dissimilar to *C. l. familiaris* and *Cuon alpinus* (1683 plots in the upper part of fig. 4.14, far above the *C. l. familiaris* and *Cuon alpinus* data clouds).

#### **Specimen 2103**

Mandible heights  $P_1$  and  $P_2$  are not conclusive about the identity of specimen 2103: it could be one of all three comparative species. Specimen 2103 only slightly overlaps with the lower part of the sample range of *C. l. lupus* for  $h-h'$   $P_1$ , but falls entirely within the *C. l. lupus* population range of tat parameter, thus it is still very likely that 2103 could be *C. l. lupus*. Specimen 2103 overlaps for most part with the upper part of the *Cuon alpinus* population range for parameter  $h-h'$   $P_2$ , but this does not significantly reduce the chance that

2103 is *Cuon alpinus*. The specimen range of 2103 falls entirely within all remaining sample and population ranges, thus from these two parameters nothing can be concluded about the identity of specimen 2103. Mean values indicate that 2103 is most similar to the average *C. l. familiaris* specimen, but this is only a circumstantial indication, not worth basing a conclusion on.

#### **Specimen 2104**

Specimen 2104 falls entirely within the sample and population ranges of both *Canis* species, which means that 2104 could very well be either of these two species. Specimen 2104 also falls entirely within the *Cuon alpinus* sample range and partly outside (above) the *Cuon alpinus* population range for  $h-h' P_2$ , based on which *Cuon alpinus* cannot yet be excluded as possibility. Fortunately, 2104 falls entirely outside (above) the *Cuon alpinus* sample and population range for  $h-h' P_1$ , thus can be concluded that 2104 is almost certainly not *Cuon alpinus* (for which there is only a 2.3% chance). Mean values and the position of 2104 with respect to the trend lines indicate that 2104 is more similar to the average *C. l. familiaris* specimen than to the average *C. l. lupus* specimen, but only based on this circumstantial indication cannot be concluded which *Canis* species 2104 is. Specimen 2104 can thus be either *C. l. familiaris* or *C. l. lupus*, but is almost certainly not *Cuon alpinus*.

#### **Specimen 2196**

An initial look at the position of 2196 in the upper part of fig 4.14, far above the *C. l. familiaris* and *Cuon alpinus* data clouds, already reveals that this specimen very probably is *C. l. lupus*. All ranges confirm this conclusion: specimen 2196 falls entirely outside (above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* and entirely within all *C. l. lupus* range. This means that 97.7% of the *C. l. familiaris* and *Cuon alpinus* specimens of their entire natural population have smaller heights below  $P_1$  and  $P_2$  than 2196. There is only a 2.3% chance that 2196 is *C. l. familiaris* or *Cuon alpinus*. Mean values, as was already obvious from the figure, (circumstantially) confirm the conclusion that specimen 2196 is *C. l. lupus*.

#### **Specimen 2329**

Specimen 2329 is a *Canis* specimen. Its specimen range falls (entirely) within the sample and population ranges of *C. l. lupus* and *C. l. familiaris* and entirely outside (above) the *Cuon alpinus* sample and population range. This means that 2329 almost certainly is not a *Cuon alpinus* specimen (for which there is only a 2.3% chance) and very probably a *C. l. lupus* or *C. l. familiaris* specimen. Specimen 2329 partly fell outside (above) the population range of *C. l. familiaris* for parameter  $h-h' P_2$ , which indicates that this specimen is quite large for a *C. l. familiaris* specimen, but this does not reduce the chance that 2329 might be *C. l. familiaris*. Mean values indicate that 2329 is most similar to the average *C. l. lupus* specimen, but neither based on this (circumstantial) evidence *C. l. familiaris* may be excluded. From these two mandibular heights cannot be concluded whether 2329 is *C. l. familiaris* or *C. l. lupus*.

#### **Specimen 2620**

Results of this specimen are conclusive: 2620 is a *C. l. lupus* specimen. There is only a 2.3% chance that 2620 is *C. l. familiaris* or *Cuon alpinus*, because 2620 falls entirely outside (above) the *Cuon alpinus* and *C. l. familiaris* sample and population ranges. Specimen 2620 even falls slightly outside (above) the *C. l. lupus* sample range for parameter  $h-h' P_2$ , which indicates that this specimen is quite large for a *C. l. lupus* specimen compared to this particular dataset (2620 does not have extremely large heights below its first two premolars compared to the entire *C. l. lupus* population, because 2620 falls within the population range). Obviously the mean values confirm that 2620 is most similar to *C. l. lupus* and that it almost certainly is not *C. l. familiaris* or *Cuon alpinus*.

#### **Specimen 3219**

From the mandible height below  $P_1$  and  $P_2$  no information can be obtained about the identity of specimen 3219. Specimen 3219 falls entirely within the sample and population ranges of all comparative material for both parameters, except the *C. l. lupus* sample range of parameter  $h-h' P_2$ , for which the overlap is only partly. But this partial overlap does not reduce the chance that 3219 might be *C. l. lupus*. Mean values and trend lines indicate that 3219 is more similar to *C. l. familiaris*, less to *Cuon alpinus* and most dissimilar to *C. l. lupus*, but based on this information no conclusion can be drawn. Specimen 3219 can thus be any of the three comparative species, based on these two parameters.

#### **Specimen 3293**

Results for this specimen are more conclusive: 3293 falls entirely outside (above) the *Cuon alpinus* sample and population ranges, which means that 97.7% of the *Cuon alpinus* specimens have smaller mandibular heights below their first two premolars than 3293. It falls entirely within the sample and population ranges of both *Canis* species. Specimen 3293 is thus a *Canis* species, but it cannot be determined which of the two species specimen 3293 is, since conclusive evidence lacks. Mean values and trend lines indicate that 3293

is most similar to the average *C. l. lupus* specimen and much less similar to *C. l. familiaris*, but this is only circumstantial evidence.

### Specimen NMR89

Interpretations of NMR89 only refer to parameter  $h-h'$   $P_2$ , since data for parameter  $h-h'$   $P_1$  are lacking for this specimen. NMR89 falls entirely within the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* and entirely outside (below) the *C. l. lupus* sample and population range, which means that NMR89 is almost certainly not a *C. l. lupus* specimen, but *C. l. familiaris* or *Cuon alpinus*. The mean value of NMR89 is most similar to the average *Cuon alpinus* specimen and less similar to the average *C. l. familiaris* specimen, but this is no conclusive evidence for the identity of NMR89. Based on these two mandible heights cannot be concluded whether NMR89 is *Cuon alpinus* or *C. l. familiaris*, only that NMR89 is not *C. l. lupus*.

### 5.3.2.2 Mandible height $h-h'$ under $P_3$ and $P_4$ (Fossil North Sea material)

All results that are discussed in this paragraph can be found in 4.2.3.2.

#### Specimen 667

Specimen 667 can either be *C. l. familiaris* or *Cuon alpinus*, because it falls entirely within the sample and population ranges of both these species. Specimen 667 only partially overlaps with the *C. l. lupus* population range of parameter  $h-h'$   $P_4$ , but this does not reduce the chance that 667 is *C. l. lupus*. Fortunately, 667 falls outside the *C. l. lupus* sample and population ranges of  $h-h'$   $P_3$ , based on which we can conclude, that there is only a 2.3% chance that 667 is *C. l. lupus*. Mean values indicate that 667 is most dissimilar to the average *C. l. lupus* specimen, thus confirm the conclusion that 667 is probably not *C. l. lupus*. Means indicate that 667 is slightly more similar to the average *C. l. familiaris* specimen than to the average *Cuon alpinus* specimen, but based on this circumstantial indication no conclusions can be drawn about the identity of specimen 667. Based on these two mandible heights it cannot be concluded whether 667 is *C. l. familiaris* or *Cuon alpinus*.

#### Specimen 1683

Specimen 1683 falls entirely outside (above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* and is thus almost certainly neither of these species. 97.7% Of all *C. l. familiaris* and *Cuon alpinus* specimens in their entire population have smaller heights below  $P_3$  and  $P_4$  than specimen 1683, thus there is only a 2.3% chance that 1683 is *C. l. familiaris* or *Cuon alpinus*. Mean values circumstantially confirm the conclusion that 1683 is a *C. l. lupus* specimen: it is most similar to the average *C. l. lupus* specimen and much less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens.

#### Specimen 2103

Specimen 2103 falls entirely within the sample and population ranges of both *Canis* species and within the sample ranges of *Cuon alpinus* for both parameters, but falls entirely outside the *Cuon alpinus* population ranges. This means that based on the sample ranges specimen 2103 could be all three comparative species, but based on the population ranges we can more or less exclude *Cuon alpinus* as possibility. Although there is only a 2.3% chance that 2103 is *Cuon alpinus*, the possibility of 2103 being *Cuon alpinus* is still present. This becomes even clearer when comparing comparative specimen *Cuon alpinus* 945 (approximate coordinates 27, 27 mm in fig. 4.15) with the *Cuon alpinus* population range. Recall from the results of the comparative material for parameters  $h-h'$   $P_3$  and  $P_4$  that this comparative specimen was the only *Cuon alpinus* that plotted far away from the rest of the specimens in the *Cuon alpinus* data cloud, far into the *C. l. lupus* data cloud. This specimen also falls outside the *Cuon alpinus* population range and is thus an example of a *Cuon alpinus* with extremely large mandible heights below  $P_3$  and  $P_4$ . Although the chance is small, that a *Cuon alpinus* shows values for a parameter that fall outside the population range for that parameter, the possibility still exists (2.3%). But the chance, that a *Cuon alpinus* shows values for all parameters taken in this study that fall outside the population ranges of these parameters, is much smaller than 2.3%. We can thus assume that 2103 is very probably not a *Cuon alpinus* specimen, but the combination with results of other parameters shall have to make this conclusion more conclusive. Mean values already circumstantially confirm that 2103 is probably not *Cuon alpinus* but *Canis*: the mean value of 2103 is most dissimilar to *Cuon alpinus* for both parameters, most similar to *C. l. familiaris* for  $h-h'$   $P_3$  and most similar to *C. l. lupus* for  $h-h'$   $P_4$ . Specimen 2103 is thus very probably not a *Cuon* specimen, but *Canis*, although based on these two mandible heights cannot be established which of the two *Canis* species.

#### Specimen 2104

Specimen 2104 falls entirely within the sample and population ranges of both *Canis* species and can thus very well be either of both species. Specimen 2104 also falls within the sample ranges of *Cuon alpinus* and partly outside (above) the *Cuon alpinus* population range for parameter  $h-h'$   $P_4$ , based on which *Cuon alpinus* cannot be excluded yet. But the fact that 2104 falls entirely outside (above) the *Cuon alpinus*

population range for  $h-h'$   $P_4$  indicates that 2104 is probably not *Cuon alpinus* (only a 2.3% chance). Mean values indicate that specimen 2104 is most similar to the average *C. l. familiaris* specimen and about equally dissimilar to *C. l. lupus* and *Cuon alpinus*. This is a slight indication towards a *C. l. familiaris* identity, but far from conclusive. Based on the mandible heights below  $P_3$  and  $P_4$  can only be concluded that specimen 2104 is very probably not *Cuon alpinus*, but either of two *Canis* species.

#### **Specimen 2196**

Specimen 2196 is almost certainly a *C. l. lupus* specimen: it falls entirely within the *C. l. lupus* sample and population ranges, but entirely outside (above) the *C. l. familiaris* and *Cuon alpinus* sample and population ranges. There is only a 2.3% chance that 2196 is *C. l. familiaris* or *Cuon alpinus*. The position of 2196 in fig. 4.16 with respect to the means of the comparative material confirms that specimen 2196 very probably is a *C. l. lupus* specimen: 2196 is most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens.

#### **Specimen 2329**

Specimen 2329 falls entirely within the *C. l. lupus* sample and population ranges for both parameters and can thus very well be this species. For *C. l. familiaris* and *Cuon alpinus* results of parameter  $h-h'$   $P_3$  are less conclusive than those of parameter  $h-h'$   $P_4$ . Based on the sample ranges of parameter  $h-h'$   $P_3$  2329 is not likely a *C. l. familiaris* specimen (2329 falls outside (above) the *C. l. familiaris* sample range), but can still be *Cuon alpinus* (it falls inside the *Cuon alpinus* sample range). Based on the population ranges of this parameter 2329 can still be a *C. l. familiaris* specimen (2329 fall partially outside this range, which does not reduce the chance of 2329 being *C. l. familiaris*), but probably not *Cuon alpinus* (it falls entirely outside (above) the *Cuon alpinus* population range). Results of parameter  $h-h'$   $P_4$  are more conclusive and indicate that specimen 2329 is very probably a *C. l. lupus* specimen: 2329 falls entirely outside (above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus*, thus there is only a 2.3% chance that 2329 is either of these two species. The mean value of 2329 is very similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens, which confirms the conclusion that 2329 is *C. l. lupus*.

#### **Specimen 2620**

Specimen 2620 only had results for parameter  $h-h'$   $P_3$ , but these are quite conclusive: 2620 falls entirely within the sample and population ranges of *C. l. lupus* and entirely outside (above) the *C. l. familiaris* and *Cuon alpinus* sample and population ranges. This means that 2620 is very probably a *C. l. lupus* specimen; there is only a 2.3% chance that 2620 is either *C. l. familiaris* or *Cuon alpinus*. The mean value of 2620 is most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens, which circumstantially confirms the conclusion that 2620 is *C. l. lupus*.

#### **Specimen 3219**

Specimen 3219 falls entirely within the sample ranges of *Cuon alpinus* and partly outside (above) the *Cuon alpinus* population range for parameter  $h-h'$   $P_3$ , based on which 3219 still can be *Cuon alpinus*. The only indication that 3219 probably is not *Cuon alpinus* comes from the population range of parameter  $h-h'$   $P_4$ : 3219 falls entirely outside (above) this population range, thus there is only a 2.3% chance that 3219 is *Cuon alpinus*. Specimen 3219 falls entirely within the sample and population ranges of both *Canis* species thus it cannot be established whether 3219 is *C. l. familiaris* or *C. l. lupus*. Mean values indicate that 3219 is more similar to *C. l. familiaris* than to *C. l. lupus*, but this is far from conclusive. Specimen 3219 can be either of the two *Canis* species.

#### **Specimen 3293**

Specimen 3293 falls entirely within the sample and population ranges of *C. l. familiaris* for parameter  $h-h'$   $P_3$ , within the sample range of *Cuon alpinus* for this parameter and partially overlaps with the *C. l. familiaris* population range for  $h-h'$   $P_4$ , which all indicates that 3293 still can be *C. l. familiaris* or *Cuon alpinus*. Specimen 3293 did fall outside the sample range of *C. l. familiaris* for  $h-h'$   $P_4$ , but 3293 can still be *C. l. familiaris* due to the overlap with the population range. Specimen 3293 falls entirely outside (above) the sample range of *Cuon alpinus* for parameter  $h-h'$   $P_4$  and outside (above) the *Cuon alpinus* population ranges for both parameters, which indicates that 3293 is very probably not *Cuon alpinus* (for which there is only a chance of 2.3%). It is very well possible that 3293 is *C. l. lupus*, since 3293 falls entirely within the sample and population ranges of this species. Although mean values indicate that 3293 is most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens, it cannot be concluded based on these two mandible heights which of the two *Canis* species specimen 3293 is.



**Specimen NMR89**

Based on parameter  $h-h'$  P<sub>3</sub> cannot be concluded yet that NMR89 is not *C. l. lupus*, because NMR89 still partly overlaps with the lower part of the *C. l. lupus* sample and population ranges, but NMR89 falls entirely outside (below) the *C. l. lupus* sample and population ranges for parameter  $h-h'$  P<sub>4</sub>. This means that there is only a 2.3% chance that NMR89 is *C. l. lupus*. Based on these mandible heights cannot be established whether NMR89 is *Cuon alpinus* or *C. l. familiaris*, because the specimen range falls within the sample and population ranges of both these species. Mean values do confirm that NMR89 is most dissimilar to the average *C. l. lupus* specimen, but neither give an indication for the identity of NMR89 (the mean value of NMR89 is most similar to the average *C. l. familiaris* specimen for parameter  $h-h'$  P<sub>3</sub> and most similar to the average *Cuon alpinus* specimen for  $h-h'$  P<sub>4</sub>). NMR89 can be either *C. l. familiaris* or *Cuon alpinus*.

**5.3.2.3 Mandible height  $h-h'$  under M<sub>1</sub> and M<sub>2</sub> (Fossil North Sea material)**

All results that are discussed in this paragraph can be found in 4.2.4.2.

**Specimen 534**

Specimen 534 falls entirely within the sample and population ranges of *C. l. lupus* and entirely outside (above) the *Cuon alpinus* sample and population ranges, which means that 97.7% of the *Cuon alpinus* specimens of the entire natural *Cuon alpinus* population have smaller heights below their molars than this specimen. Specimen 534 is thus very likely not *Cuon alpinus* (for which there is only a 2.3% chance), but could very well be *C. l. lupus*. This specimen falls only partly outside the *C. l. familiaris* sample range, based on which this species cannot be excluded as possible identity for 534 yet, but 534 also falls entirely outside (above) the *C. l. familiaris* population range, thus we can conclude that there is only a 2.3% chance that 534 is *C. l. familiaris*. The fact that the mean value of 534 is most similar to the average *C. l. lupus* specimen (circumstantially) supports the conclusion that specimen 534 is very probably *C. l. lupus*.

**Specimen 535**

Specimen 535 falls entirely outside the *Cuon alpinus* sample and population ranges, thus there is only a 2.3% chance that 535 is *Cuon alpinus*. But it cannot be concluded, whether 535 is *C. l. familiaris* or *C. l. lupus*, because 535 falls entirely within the sample and population ranges of both *Canis* species. Mean values indicate that 535 is most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* specimen, but based on solely this indication the identity of specimen 535 cannot be established. Specimen 535 can either be *C. l. familiaris* or *C. l. lupus*.

**Specimen 667**

Specimen 667 falls outside the *C. l. lupus* sample range for parameter  $h-h'$  M<sub>1</sub>, but inside corresponding population range, thus based on this range 667 can still be *C. l. lupus*. Specimen 667 also falls within the sample and population ranges of *C. l. lupus* for parameter  $h-h'$  M<sub>2</sub> and within the *C. l. familiaris* sample and population ranges for both parameters, thus based on the mandibular heights below the first two molars specimen 667 can be either of the two *Canis* species. Means indicate that 667 is more similar to *C. l. familiaris* than to *C. l. lupus*, but this is no conclusive evidence. Specimen 667 falls slightly outside (above) the *Cuon alpinus* population range for parameter  $h-h'$  M<sub>1</sub> and entirely within the *Cuon alpinus* sample ranges for both parameters, based on which *Cuon alpinus* cannot be excluded yet. But 667 also falls entirely outside the *Cuon alpinus* population range for parameter  $h-h'$  M<sub>2</sub>, based on which can be concluded that 667 is very probably not a *Cuon alpinus* specimen (for which there is only a 2.3% chance). Specimen 667 is thus either *C. l. familiaris* or *C. l. lupus*.

**Specimen 1683**

Specimen 1683 falls entirely within the *C. l. lupus* sample and population ranges and entirely outside (above) the *C. l. familiaris* and *Cuon alpinus* sample and population ranges, thus there is only a 2.3% chance that 1683 is *C. l. familiaris* or *Cuon alpinus*. Mean values support the conclusion that 1683 is *C. l. lupus*: the mean value of 1683 is most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens (fig. 4.18).

**Specimen 2103**

Specimen 2103 falls outside the *Cuon alpinus* sample and population ranges, thus there is only a 2.3% chance that 2103 is *Cuon alpinus*. Specimen 2103 is thus a *Canis* specimen, but it cannot be concluded which of the two species, since 2103 falls entirely within the sample and population ranges of both *Canis* species. Mean values are also inconclusive, since 2103 is most similar to *C. l. familiaris* for one parameter and to *C. l. lupus* for the other. Specimen 2103 is thus almost certainly not a *Cuon alpinus* specimen, but either of two *Canis* species.

### **Specimen 2104**

Specimen 2104 only partially overlaps with the sample range of *C. l. lupus* for parameter  $h-h'$   $M_1$  and the *Cuon alpinus* population range for parameter  $h-h'$   $M_2$ , but this does not reduce the chance that 2104 is either of these two species. Since 2104 also falls entirely within the *C. l. lupus* population range for parameter  $h-h'$   $M_1$  and entirely within the *C. l. lupus* sample and population ranges for parameter  $h-h'$   $M_2$ , 2104 can still be *C. l. lupus*. Specimen 2104 also could be a *C. l. familiaris* specimen, since it falls entirely within the *C. l. familiaris* sample and population ranges. Specimen 2104 also falls within the sample ranges of *Cuon alpinus*, based on which 2104 could still be a *Cuon alpinus* specimen. But it falls entirely outside (above) the *Cuon alpinus* population range for parameter  $h-h'$   $M_1$ , thus it can be concluded that there is only a 2.3% chance that specimen 2104 is *Cuon alpinus*. Mean values indicate that 2104 is most similar to the average *C. l. familiaris* specimen and most dissimilar to the average *C. l. lupus* specimen, but this is no conclusive evidence. Specimen 2104 can be either of the two *Canis* species.

### **Specimen 2196**

Mandibular heights below  $M_1$  and  $M_2$  indicate that specimen 2196 is very probably a *C. l. lupus* specimen: 2196 falls entirely within the *C. l. lupus* sample and population ranges and entirely outside (above) the *Cuon alpinus* sample and population ranges and *C. l. familiaris* population ranges. There is thus only a 2.3% chance that 2196 is *Cuon alpinus* or *C. l. familiaris*. Mean values indicate that 2196 is most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* specimen, circumstantially supporting the conclusion that 2196 is *C. l. lupus*.

### **Specimen 2329**

Specimen 2329 falls entirely outside (above) the *Cuon alpinus* sample and population ranges for both parameters and the *C. l. familiaris* population range for parameter  $h-h'$   $M_1$ , based on which can be concluded that 2329 is very probably neither of these species, because there is only a 2.3% chance that 2329 is *Cuon alpinus* or *C. l. familiaris*. Mean values support the conclusion that 2329 is *C. l. lupus*, since the mean value of 2329 is most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens.

### **Specimen 3219**

Specimen 3219 falls entirely outside (above) the *Cuon alpinus* sample and population ranges for parameter  $h-h'$   $M_1$  and entirely outside the *Cuon alpinus* population range for parameter  $h-h'$   $M_2$ . Based on this information we can conclude that 3219 is very probably not a *Cuon alpinus* specimen (for which there is only a 2.3% chance). Specimen 3219 falls entirely within the sample and population range of both *Canis* species, thus, although the mean value of 3219 is most similar to the average *C. l. familiaris* specimen and most dissimilar to the average *C. l. lupus* specimen, it cannot be concluded whether 3219 is *C. l. familiaris* or *C. l. lupus*.

### **Specimen 3293**

Specimen 3293 falls within the sample and population ranges of both *Canis* species (although only partially within the *C. l. familiaris* population range for  $h-h'$   $M_1$ ), thus 3293 can either be *C. l. familiaris* or *C. l. lupus*. This specimen falls entirely outside (above) the *Cuon alpinus* sample and population ranges, thus there is only a 2.3% chance that 3293 is *Cuon alpinus*. Mean values indicate that 3293 is most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* specimen, but this is only circumstantial. Specimen 3293 is thus almost certainly not *Cuon alpinus*, but it cannot be determined which of the two *Canis* species it is.

### **Specimen NMR89**

NMR89 falls entirely within the sample and population range of both *Canis* species and entirely outside (above) the *Cuon alpinus* sample and population ranges. There is thus only a 2.3% chance that NMR89 is *Cuon alpinus*, but it cannot be concluded which of the two *Canis* species NMR89 is. Mean values are also inconclusive, since NMR89 is most similar to *C. l. familiaris* for one parameter and to *C. l. lupus* for the other. Specimen NMR89 is thus almost certainly not a *Cuon alpinus* specimen, but either of two *Canis* species.

### **Values from literature**

For the parameter 'Mandible height  $h-h'$   $M_1$ ' values of eleven *Cuon alpinus* specimens from literature were added to the comparative dataset and the fossil North Sea specimens were compared to the newly calculated sample and population ranges (table IX.3, IX.4 and appendix XII). For specimens 1683, 2196, 2329 and 3293 previous results and thus interpretations are confirmed by the new extended dataset: these specimens fall entirely outside the new *Cuon alpinus* sample and population ranges, which means that there is only a 2.3% chance that these specimens are *Cuon alpinus* and thus very probably belong to the genus *Canis*. For specimen 535 results were slightly different, but this does not change the final conclusion: 535 still falls entirely outside the new population range, thus this specimen is very probably not *Cuon alpinus* (for

which the chance is still 2.3%). Specimens 667 and 2104 both fell originally within the sample range of *Cuon alpinus* and partly outside the corresponding population range. It was concluded that partial overlap does not reduce the chance that these specimens are *Cuon alpinus*, which is proven correct by the new comparisons, which show that 667 and 2104 fall entirely within both *Cuon alpinus* ranges of the extended dataset. This indeed means that these two specimens still can belong to the *Cuon alpinus* genus. Specimens 2103, 3219 and NMR89 originally fell outside both *Cuon alpinus* ranges, based on which was concluded that there is only a 2.3% chance that these specimens are *Cuon alpinus*, but they fall entirely within the *Cuon alpinus* sample and population ranges for the new dataset. Thus based on the new, larger *Cuon alpinus* comparative dataset we have to conclude that this chance is much larger and that specimens 2103, 3219 and NMR89 can very well be *Cuon alpinus*.

### 5.3.3 Ratios of mandibular length, width and height

#### 5.3.3.1 Comparative material

Results indicated that for the average *C. l. familiaris* specimen mandible lengths, widths and heights are reduced in proportion to *C. l. lupus* in similar amounts (4.2.5.1). This means that *Canis* mandibles have approximately the same proportions and that size is the major difference between *C. l. lupus* and *C. l. familiaris* mandibles. There is slightly more reduction in width and height than in length, which means that a minor difference between the two *Canis* species is that *C. l. familiaris* mandibles are slightly more fragile than *C. l. lupus* mandibles (because they are relatively thinner than *C. l. lupus* mandibles). One could question if this trend is significant, because percentages are very similar. But the higher amount of fragility of *C. l. familiaris* was also obvious from initial qualitative observations, thus in general *C. l. familiaris* mandibles are indeed slightly more fragile than *C. l. lupus*. The observance of a similar amount of reduction or a slight trend towards higher fragility indicates that a specimen could be *C. l. familiaris*. For *Cuon alpinus* a more obvious trend is visible: the mandible width is reduced less in size than the length and height, as a result of which *Cuon alpinus* mandibles are sturdier than *Canis* mandibles (4.2.5.1). This quantification confirmed initial observations and we can conclude that reduction in size relative to the average comparative *C. l. lupus* reference value whereby width (and possibly also height, according to Pérez Ripoll et al. (2010)) is more reduced than length indicates that the specimen could be *Cuon alpinus*.

Note that these ratio calculations are based on the comparison of average *C. l. familiaris* and *Cuon alpinus* values with an average *C. l. lupus* reference value and thus on general and 'normal' trends for these species. Results of this parameter do thus not entirely exclude the possibility of *Cuons* that are more fragile or *C. l. familiaris* specimens that are sturdier than the average *C. l. lupus* specimen, although qualitative observations indicated that this is unlikely to occur. Based on this parameter we can thus conclude, that it is more likely that a specimen that is reduced in size and more fragile (or sturdy) than the average *C. l. lupus* specimen is *C. l. familiaris* (*Cuon alpinus*), but *Cuon alpinus* (*C. l. familiaris*) cannot be entirely excluded as possibility.

So far only the interpretation of reduction trends is discussed, while increase is also possible (4.2.5.1). For all three parameters (Alveolar length  $P_1-M_2$ , Width of the mandible  $i-i'$  and Height  $h-h'$   $P_3$ ), comparative *Cuon alpinus* and *C. l. familiaris* specimens barely exceed the *C. l. lupus* mean (figures 4.3, 4.11 and 4.15). Since this *C. l. lupus* mean is the reference point, *Cuon alpinus* and *C. l. familiaris* will almost never show an increase in percentages, while any arbitrarily chosen *C. l. lupus* specimen shall approximately have 50% chance of showing an increase in percentages and approximately 50% chance of showing a decrease in percentages. All three comparative species have a significant amount of specimens that will show reduction in mandible length, width and height compared to the reference value, thus there cannot be distinguished between *C. l. familiaris*, *C. l. lupus* and *Cuon alpinus* solely based on the fact that there is reduction. Because approximately 50% of the *C. l. lupus* specimens also will show reduced size (and possibly also fragility) one cannot entirely exclude *C. l. lupus* when reduction and fragility is observed, only when a clear fragility trend is observed *C. l. familiaris* is a more likely option. Since *C. l. lupus* is the only species that shows an increase in mandible length, width and height compared to the reference value, specimens that show an increase can be assigned to *C. l. lupus*.

Probable causes for the different trends that were observed between this dataset and that of Ripoll et al. (2010) are that the Ripoll data were derived from the comparison of one *Cuon alpinus* specimen with one *C. l. lupus* specimen, whereas in this dataset averages were used of multiple specimens. Also, the parameters that were used to represent mandible width and height in this study were taken at slightly different positions on the mandibles than the parameters of Ripoll.

### **5.3.3.2 Fossil North Sea material**

All results that are discussed in this paragraph can be found in 4.2.5.2.

#### **Specimen 535 and NMR90**

These specimens both show a decrease in mandible width compared to the average comparative *C. l. lupus* reference value, but lack values for length and height. Based on solely a decrease in width nothing (quantitative) can be concluded about the identity of these two fossil North Sea specimens. (Note that a conclusion could be derived from qualitative observations of the mandible ratios of specimen NMR90 in 5.2.1.1)

#### **Specimen 667**

In this specimen width is much less reduced in size compared to the average comparative *C. l. lupus* reference value than length and height (a typical *Cuon alpinus* trend), but the height is more reduced than the length (a more typical *C. l. familiaris* trend). These results are ambiguous and more or less cancel each other out. The mandible is only slightly sturdier than the average *C. l. lupus* specimen, because the effect of the width is slightly higher than the effect of height (the difference length-height is less than the difference length-width). These observations indicate that specimen 667 is probably not a *C. l. lupus* specimen, but either *C. l. familiaris* or *Cuon alpinus*.

#### **Specimen 1683, 2196 and 2620**

These three specimens all showed an increase in mandible length, width and height compared to the average *C. l. lupus* reference value and are thus very likely *C. l. lupus* specimens. Specimen 2620 shows less increase in width than in length and height and is thus more fragile than the average *C. l. lupus* specimen, but the larger mandible values are more conclusive than the fragility trend. Also specimen 2620 is very likely *C. l. lupus*.

#### **Specimen 2103**

This specimen shows reduction in all three parameters, but relatively more reduction in width. This means that this hemimandible is more fragile than the average *C. l. lupus* specimen and is thus likely *C. l. familiaris* (although *C. l. lupus* cannot entirely be excluded). Specimen 2103 is very probably not *Cuon alpinus*, because the observed fragility trend is opposite to the trend observed in an average *Cuon alpinus* specimen.

#### **Specimen 2104**

Specimen 2104 shows reduction in length, width and height in similar amounts (although width is slightly more reduced than length and height). This trend is similar to the trend observed in *C. l. familiaris*, although *C. l. lupus* cannot be excluded as possibility, and unlike the *Cuon alpinus* trend. Specimen 2104 is thus probably not *Cuon alpinus*, but *Canis*.

#### **Specimen 2329**

Specimen 2329 shows only a very slight increase in length, has the same height as the average *C. l. lupus* value and shows a decrease in width. This specimen is very comparable in size to the average *C. l. lupus* specimen and could very well be this species. But this specimen is also more fragile, because it shows a reduction in width and not in length and height. This indicates that specimen 2329 also could be *C. l. familiaris*, but probably not *Cuon alpinus*. Specimen 2329 is thus very likely either of both *Canis* species.

#### **Specimen 3219**

This specimen shows reduction in length, width and height in similar amounts, like the *C. l. familiaris* trend, and is thus probably not a *Cuon alpinus* specimen. Since it is expected that approximately 50% of the *C. l. lupus* specimens also show reduction in size relative to the average *C. l. lupus* value, this specimen could also be *C. l. lupus*. Based on these ratios we can conclude that specimen 3219 is probably not *Cuon alpinus*, but either of the two *Canis* species.

#### **Specimen 3293**

The length, width and height ratios of this specimen are very comparable to the average *C. l. lupus* specimen and there are no clear trends towards fragility or sturdiness. Specimen 3293 is thus probably not *Cuon alpinus*. This specimen is more likely *C. l. lupus* than *C. l. familiaris*, because length and width are both slightly increased, but *C. l. familiaris* cannot be excluded as possibility, because not all three parameters show an increase (the height is reduced). Specimen 3293 can be either of the two *Canis* species.

**Specimen NMR89**

This specimen has a length that is comparable to the average *C. l. lupus* specimen, but is much smaller and much more reduced in height. This trend is opposite the trend observed in *Cuon alpinus* by Pérez Ripoll et al. (2010). Moreover, this reduction of height indicates that NMR89 is more fragile than the average *C. l. lupus* specimen. NMR89 is thus probably not a *Cuon alpinus* specimen, but could be either *C. l. familiaris* (based on the fragility trend) or *C. l. lupus* (which cannot be excluded since the length is slightly increased).

**5.3.4 Conclusions section ‘Mandible (width, height and ratios)’**

In this paragraph (preliminary) conclusions about the identity of the 13 fossil North Sea specimens will be drawn, based on the combined conclusions of the individual parameters that were presented in this second ‘Mandible (width, height and ratios)’ section. For an overview of all results and interpretation thereof, see appendix XII.

**Specimen 534 (*C. l. lupus*)**

This fossil North Sea specimen could only be measured for 1 of the 9 subparameters of this section (‘Distance *h-h*’ under  $M_2$ , table XII.1). Based on this parameter specimen 534 could be identified as *C. l. lupus* with a 97.7% confidence interval, confirming the conclusion of the ‘Mandible length’ section.

**Specimen 535 (*Canis*)**

Specimen 535 could only be measured for 3 out of 9 subparameters of the ‘Mandible (width, height and ratios)’ section (‘Width of the mandible’ *i-i*’ and ‘Distance *h-h*’ under  $M_1$  and  $M_2$ , table XII.1). Based on the mandible width specimen 535 could still be one of all three comparative (sub)species and the mandible heights under the two molars could only identify 535 on genus level: specimen 535 is *Canis* and not *Cuon alpinus* (97.7% confidence interval). The extended dataset (that includes 11 *Cuon alpinus* values from literature) for parameter ‘Distance *h-h*’ under  $M_1$  confirmed that 535 is not *Cuon alpinus* (again with a 97.7% confidence interval), because even with 11 extra *Cuon alpinus* values the mandible height of specimen 535 under its first molar still was larger than all comparative *Cuon alpinus* specimens. Based on the parameters in this second section specimen 535 can thus only be identified on genus level, while in the ‘Mandible length’ section one parameter indicated that this specimen is *C. l. lupus*. The evidence for a *C. l. lupus* identity so far only comes from one parameter (Alveolar length  $M_1$ - $M_2$ ) and is thus not (yet) very solid.

**Specimen 667 (*C. l. familiaris*)**

Specimen 667 was measured for all 9 subparameters of the ‘Mandible (width, height and ratios)’ section (table XII.2). All 9 parameters indicated that a *C. l. familiaris* identity is very well possible for specimen 667. Based on only one subparameter (‘Mandible height *h-h*’ under  $M_2$ ) we can conclude that specimen 667 is not *Cuon alpinus* (with a 97.7% confidence interval). A *C. l. lupus* identity for 667 was excluded by three parameters (‘Mandible height *h-h*’ under  $P_2$  and  $P_3$  and the mandible ratios). Because two of these parameters are quantitative (have a statistical confidence interval), the chance that 667 is *C. l. lupus* is slightly less than 2.3%. All other parameters were not indicative of the identity of this fossil North Sea specimen. Based on the combined evidence of all parameters in this section specimen 667 can be assigned to *C. l. familiaris* with a 97.7% confidence interval, which confirms the conclusion of the ‘Mandible length’ section.

**Specimen 1683 (*C. l. lupus*)**

This fossil North Sea specimen was also measured for all 9 parameters of the ‘Mandible (width, height and ratios)’ section (table XII.2). All 9 parameters indicated that a *C. l. lupus* identity is very well possible for specimen 667 (no ‘problems’ (red characters) are encountered in this column in table XII.2). Only the parameter ‘Width of the mandible’ *k-k*’ left open the possibility that 1683 is *C. l. familiaris*, but all other subparameters of this section assigned specimen 1683 to *C. l. lupus* with a 97.7% confidence interval. The exclusion of *Cuon alpinus* as possibility was extra confirmed by the extended dataset (that includes 11 *Cuon alpinus* values from literature for parameter ‘Mandible height *h-h*’ under  $P_2$ ). This second section provided very strong evidence for a *C. l. lupus* identity of specimen 1683.

**Specimen 2103 (*Canis*)**

Specimen 2103 was measured for all 9 parameters of the ‘Mandible (width, height and ratios)’ section (table XII.3). Mandible ratios already indicated that specimen 2103 is not likely a *Cuon alpinus* specimen and 3 quantitative subparameters (‘Mandible height *h-h*’ under  $P_3$ ,  $P_4$  and  $M_2$ ) confirmed that 2103 is not *Cuon alpinus* with a 97.7% confidence interval (‘Mandible height *h-h*’ under  $M_1$  also initially excluded *Cuon alpinus* as possibility, but this conclusion had to be revised based on the extended dataset (that includes 11 *Cuon* values from literature), which did overlap with the 2103 specimen range). Mandible ratios also indicated that specimen 2103 is less likely *C. l. lupus* than *C. l. familiaris* and mandible width *i-i*’

indicates that the mandible of 2103 is quite small for a *C. l. lupus* specimen, but none of the 9 parameters in this second section indicate that *C. l. lupus* can be excluded as possible identity for 2103 with a 97.7% confidence interval. Based on the combined evidence of this second section we can only identify 2103 on genus level: specimen 2103 is a *Canis* specimen and not *Cuon* (with a 97.7% confidence interval). This section is less conclusive than the first section, which indicated with a 97.7% confidence interval that specimen 2103 is a *C. l. familiaris* specimen.

#### **Specimen 2104 (*Canis*)**

This fossil North Sea specimen was also measured for all 9 parameters of the 'Mandible (width, height and ratios)' section (table XII.3). Mandible ratios indicated (only on genus level) that 2104 is less likely *Cuon* than *Canis* and subparameters 'Mandible height *h-h*' under  $P_1$  and  $P_4$  confirmed with a 97.7% confidence interval that specimen 2104 indeed is not *Cuon alpinus*. All other parameters were not indicative of the identity of 2104 and all parameters left open the possibility that specimen 2104 is either *C. l. familiaris* or *C. l. lupus*. Based on the combined evidence of this second section the identity of specimen 2104 can thus only be established on genus level (2104 is not a *Cuon* specimen, but *Canis*) on the contrary to the previous section in which was concluded with a 97.7% confidence interval that specimen 2104 belongs to the subspecies *C. l. familiaris*.

#### **Specimen 2196 (*C. l. lupus*)**

Specimen 2196 was measured for all 9 parameters of the 'Mandible (width, height and ratios)' section (table XII.4). All 9 parameters in this section indicated that specimen 2196 is not *C. l. familiaris* or *Cuon alpinus* (with a 97.7% confidence interval) and left open the possibility of a *C. l. lupus* identity. Mandible width *k-k'* even indicated that specimen 2196 is quite large for a *C. l. lupus* specimen. That this fossil specimen is not *Cuon alpinus* was extra confirmed by the extended dataset of parameter 'Mandible height *h-h*' under  $P_{M1}$  that includes 11 *Cuon alpinus* values from literature. This second section is even more conclusive about the identity of fossil specimen 2196 than the first section and confirms the conclusion that specimen 2196 is a *C. l. lupus* specimen.

#### **Specimen 2329 (*C. l. lupus*)**

This fossil North Sea specimen was also measured for all 9 parameters of the 'Mandible (width, height and ratios)' section (table XII.4). A *Cuon alpinus* identity for this specimen was excluded based on all parameters in this section, with a 97.7% confidence interval (and for the mandible height under  $M_1$  results were confirmed by the extended dataset). A *C. l. familiaris* identity could also be excluded with a 97.7% confidence interval, but only based on two quantitative subparameters ('Mandible height *h-h*' under  $P_4$  and  $M_1$ ). There were no 'problems' encountered for *C. l. lupus*. We can conclude based on the combined evidence of all parameters in this section that specimen 2329 can be assigned to *C. l. lupus* with a 97.7% confidence interval, which confirms the conclusion obtained in the first section.

#### **Specimen 2620 (*C. l. lupus*)**

Specimen 2620 could only be measured for 6 of the 9 parameters in this section (table XII.5). Mandible ratios already indicated that specimen 2620 is not likely a *C. l. familiaris* or *Cuon alpinus* specimen and this was confirmed by the 5 quantitative parameters in this section: based on the parameters 'Width of the mandible' *i-i'* and *k-k'* and 'Mandible height *h-h*' under  $P_1$ ,  $P_2$  and  $P_3$  a *Cuon alpinus* identity can be excluded for specimen 2620 with a confidence interval of 97.7% and based on the parameters 'Mandible height *h-h*' under  $P_1$ ,  $P_2$  and  $P_3$  also a *C. l. lupus* identity can be excluded with a confidence interval of 97.7%. We can thus conclude, based on the combined evidence in this section, that specimen 2620 is a *C. l. lupus* specimen, which confirms the conclusion of the first section.

#### **Specimen 3219 (*Canis*)**

This fossil North Sea specimen was measured for all 9 parameters of the 'Mandible (width, height and ratios)' section (table XII.5). A *Cuon alpinus* identity could be excluded based on the parameters 'Width of the mandible' *k-k'*, 'Mandible height *h-h*' under  $P_4$  and  $M_2$  and the mandible ratios. However, all parameters in this section left open the possibility of either a *C. l. familiaris* or a *C. l. lupus* identity of specimen 3219. Based on the combined evidence of all parameters in this section we can only identify specimen 3219 on genus level: 3219 is assigned to *Canis* with a 97.7% confidence interval. Also for the first section 3219 could not be assigned to *C. l. familiaris* or *C. l. lupus*. There is still no solid evidence for the identity of specimen 3219 on subspecies level.

**Specimen 3293 (*Canis*)**

This specimen was measured for 8 parameters of the 'Mandible (width, height and ratios)' section (table XII.6), but could only be identified on genus level. Based on all parameters we can conclude that specimen 3293 is not *Cuon alpinus* with a 97.7% confidence interval, but the possibility that 3293 is either *C. l. familiaris* or *C. l. lupus* is left open in this section, on the contrary to the previous section in which was concluded with a 97.7% confidence interval that specimen 3293 is a *C. l. lupus* specimen.

**Specimen NMR89 (*C. l. familiaris*)**

NMR89 was measured for 7 parameters of this section (table XII.6). Based on two parameters ('Mandible height  $h-h''$ ' under  $M_2$  and the mandible ratios) a *Cuon alpinus* identity could be excluded with a 97.7% confidence interval. A *C. l. lupus* identity was excluded based on two quantitative subparameters ('Mandible height  $h-h''$ ' under  $P_2$  and  $P_4$ ). On the contrary to the previous section (where was concluded with a 97.7% confidence interval that NMR89 is *C. l. lupus*) conclusions in this section point towards a *C. l. familiaris* identity, with 97.7% confidence.

**Specimen NMR90 (?)**

Specimen NMR90 was only measured for one parameter in this section ('Width of the mandible'  $i-i'$ ) and this parameter was entirely inconclusive about the identity of the fossil specimen: the specimen range of NMR90 falls within all ranges of all three comparative (sub)species (table XII.7). On the contrary to the previous section, where was concluded with a 97.7% confidence interval that NMR90 is a *C. l. familiaris* specimen, no conclusion can be drawn about the identity of specimen NMR90 based on this section.

## 5.4 Ramus

### 5.4.1 Distance *a-d* and *e-e'*

Since all distances have similar results (4.3.1), *a-d* and *e-e'* will be interpreted together: if is not explicitly stated otherwise, in each paragraph conclusions hold true for both parameters. Only where the parameters do not have the same results, results will be mentioned separately.

#### 5.4.1.1 Comparative material

Everything that could be interpreted about the comparative material was already done for previous parameters (see previous paragraphs and mainly 5.2.1.1). Results of the comparative material for these two parameters are as expected (thus similar to previous parameters): there are no remarkable observations (4.3.1.1). There is no need to interpret the comparative material for these parameters separately.

#### 5.4.1.2 Fossil North Sea material

All results that are discussed in this paragraph can be found in 4.3.1.2.

#### Specimen 534

Specimen 534 falls entirely within the sample and population ranges of *C. l. lupus*, entirely outside (above) the *Cuon alpinus* sample and population ranges for both parameters and entirely outside (above) the *C. l. familiaris* sample and population range for parameter *a-d*. If the values for *a-d* and *e-e'* were not estimated we could conclude based on this information that there is only a 2.3% chance that specimen 534 is *C. l. familiaris* or *Cuon alpinus* and very likely is *C. l. lupus*. But the values for this specimen are estimated, thus the specimen range could have been slightly smaller or larger if the actual ramus of 534 could have been measured. Nonetheless it is very probable that the ramus of 534, even if the values would have been slightly smaller, still would have values that fall outside the *C. l. familiaris* and *Cuon alpinus* ranges, because the distance between the minimum value of the specimen range and the *Cuon alpinus* and *C. l. familiaris* maxima are quite significant. It is thus not possible to conclude that there is only a 2.3% chance that 534 is *C. l. familiaris* or *Cuon alpinus*, but it is still very likely that 534 is *C. l. lupus* and not *Cuon alpinus* or *C. l. familiaris*. Mean values support this conclusion (the mean value of 534 is most similar to the average *C. l. lupus* specimen and much less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens).

#### Specimen 667

For this specimen the values were not estimated, but nothing conclusive can be stated about the identity of 667 based on these two parameters. The specimen range of this specimen namely falls in all sample and population ranges of all three comparative species, although only partly within the *Cuon alpinus* population ranges. This partial overlap does not reduce the chance that 667 is *Cuon alpinus*. Mean values indicate that 667 is most similar to the average *C. l. familiaris* specimen, less similar to the average *Cuon alpinus* specimen and most dissimilar to the average *C. l. lupus* specimen, but this is not conclusive evidence. Based on parameters *a-d* and *e-e'* 667 could still be *Canis* or *Cuon alpinus*.

#### Specimen 2103 and 2104

Parameters *a-d* and *e-e'* are also not informative at all for these two specimens. Both specimen falls in all ranges, except that specimen 2103 partly falls outside (below) the *C. l. lupus* sample and population range for *e-e'* and that specimen 2104 partially falls outside (below) the *C. l. lupus* sample and population ranges for both parameters. Since, both specimens still partially overlap with the *C. l. lupus* ranges, this species cannot be excluded as possibility. Mean values indicate that these two specimens are most similar to the average *C. l. familiaris* specimen, less similar to the average *Cuon alpinus* specimen and most dissimilar to the average *C. l. lupus* specimen, but this is no conclusive evidence. Based on the distances *a-d* and *e-e'* specimens 2103 and 2104 could still be either *Canis* or *Cuon*.

#### Specimen 2196

Results for this specimen are more conclusive. Specimen 2196 falls entirely outside (above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* and even partly outside (above) the *C. l. lupus* population ranges. The values for specimen 2196 for distances *a-d* and *e-e'* were estimated from a comparative specimen, but the distances between the minimum of the specimen range and the maxima of the *C. l. familiaris* and *Cuon alpinus* ranges are very large. It is thus very likely that the actual ramus of 2196 also would have had values that fall outside the ranges of these two species. Moreover, until this point all specimens that were quite large and exceeded the *C. l. lupus* range, were all identified as *C. l. lupus* specimens; it would be very unusual for a *C. l. familiaris* or *Cuon alpinus* specimen to be larger than all comparative *C. l. lupus* specimens. It is thus valid to assume that there is only a 2.3% chance that 2196 is *C. l. familiaris* or *Cuon alpinus*. Mean values (circumstantially) support the conclusion that 2196 is *C. l. lupus*:



2196 is most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens.

### Specimen 2329

Specimen 2329 is almost certainly a *C. l. lupus* specimen: it falls entirely within the sample and population ranges of *C. l. lupus*, entirely outside (above) the sample and population ranges of *Cuon alpinus* for both parameters, outside (above) the sample and population ranges of *C. l. familiaris* for *a-d* and outside (above) the *C. l. familiaris* population range of *e-e'*. There is thus only a 2.3% chance that this specimen is *C. l. familiaris* or *Cuon alpinus*. Mean values indicate that 2329 is most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens, supporting the conclusion that 2329 is *C. l. lupus*.

### Specimen NMR90

Values for distances *a-d* and *e-e'* were estimated for NMR90.

NMR90 falls entirely within all ranges except the *Cuon alpinus* population range of parameter *e-e'*, but the distance between the maximum of the population range and the minimum of the specimen range is not very large. Since this minimum is based on an estimate, the actual minimum value of the NMR90 specimen range could have been slightly lower and overlap with the *Cuon alpinus* population range. Also because NMR90 does fall within the other *Cuon alpinus* ranges, *Cuon alpinus* cannot be excluded as possibility. Mean values are also not very informative, since the trends to which species NMR90 is most similar are completely reversed for both parameters. Based on *a-d* and *e-e'* specimen NMR90 could still be either *Canis* or *Cuon alpinus*.

Results of the parameters *a-d* and *e-e'* were not very conclusive: for only 3 out of 7 specimens they provided information about the identity of these specimens. This could also partly be caused by the fact that these two parameters are among the parameters with the highest measuring error (table 2.1), which possibly causes the ranges to be large.

## 5.4.2 Aboral border of the ramus

### 5.4.2.1 Comparative material

Discussed results can be found in 4.3.3.1. As Pérez Ripoll et al. (2010) observed, an aboral border facing the front is more common in *Cuon alpinus* than in *Canis*. The only *Canis* specimen that has a front facing aboral border is a recent *C. l. familiaris* specimen from Suriname, while all *C. l. lupus* and fossil *C. l. familiaris* specimens from the Netherlands showed a vertical or rear facing aboral border. Although a front facing border in *C. l. familiaris* is thus very rare, this species cannot entirely be excluded as possibility. A fossil specimen with a front facing aboral border can thus be *Cuon alpinus*, not *C. l. lupus* and very probably also not *C. l. familiaris*. An aboral border facing the rear is very common in both *Canis* species, but quite rare in *Cuon alpinus*. When a rear facing aboral border is encountered in a specimen, it is thus more likely that this specimen is *Canis* than *Cuon alpinus*, although *Cuon alpinus* cannot entirely be excluded as possibility. This parameter is thus more an indication for the probable identity of the fossil North Sea specimens than solid evidence. Moreover this parameter only can distinguish on genus level: *Canis* or *Cuon*. A third option is possible: an aboral border neither facing the front or rear. Most *Cuon alpinus* and *C. l. lupus* specimens and a significant part of the *C. l. familiaris* mandibles have an aboral border facing vertical, thus this position of the aboral border is not typical for one of the three species. One cannot distinguish between the three comparative species when this option is encountered.

### 5.4.2.2 Fossil North Sea material

Results of the 13 fossils can be found in 4.3.3.2. Only in fossil North Sea specimens 534, 667, 2103, 2104 and 2329 a sufficiently large part of the ramus is present to see in which direction the aboral border is facing. In all five specimens the aboral border of the ramus faces the rear. It is thus more likely that these specimens are *Canis* than that they are *Cuon alpinus*, but *Cuon alpinus* cannot entirely be excluded as possibility. This parameter is only a confirmation of what was already known from previously discussed parameters.

## 5.4.3 Anterior border of the coronoid process

### 5.4.3.1 Comparative material

Results can be found in 4.3.4.1. We observed that in the comparative dataset of this study the anterior border of *Canis* specimens typical is small and clearly sticks out compared to the rest of the hemimandible as a distinct ridge, while in *Cuon alpinus* the border is broader, more rounded and less distinct. Not only are these appearances of the anterior border typical for *Canis* and *Cuon*, but the typical *Canis* border never occurs in *Cuon* and the typical *Cuon* border never occurs in *C. l. lupus*. This means that the observation of a thin anterior border in a fossil specimen is a strong indication that that specimen belongs to the genus *Canis* and the observation of a thick anterior border is a strong indication that the specimen is not *C. l. lupus*. Since there are a few *C. l. familiaris* specimens that also have a thick anterior border like *Cuon alpinus*, it cannot be excluded that a fossil specimen with a thick border is *C. l. familiaris*, but it is more likely that the specimen is *Cuon alpinus*. Apart from the (rare) occurrence of a thick border in *C. l. familiaris*, there are no significant differences between the two *Canis* species and one cannot distinguish between *C. l. lupus* and *C. l. familiaris* based on this parameter. There are also many specimens of all three comparative species that do not have an anterior border that is typical for *Canis* or *Cuon*, thus based on this non-typical border a specimen cannot be assigned to either genus. This parameter can thus be used as indicator of the genus, but only if a typical appearance of the anterior border is present.

### 5.4.3.2 Fossil North Sea material

For the results of the fossil specimens, see 4.3.4.2.

#### Specimens 534 and 2104

Specimen 534 does not show a small and distinct ridge as is observed typical *Canis* specimens, but although the ridge is quite broad, also does not resemble the typical rounded *Cuon* border. Solely based on this parameter it is thus not very clear to which genus specimen 534 should be assigned: the appearance of the anterior border of 534 is quite vague. Moreover, we know from previous parameters that this specimen is very probably not *Cuon alpinus* and more likely a *Canis* specimen (as can also be seen from the overall appearance and size of the hemimandible). Thus although the anterior border was classified as thick we cannot conclude that 534 is probably *Cuon alpinus*. Based on solely this parameter no clear conclusion can be drawn for specimen 534. Specimen 2104 also has no typical appearance of its anterior border and was classified as average: the border is not thin like other *Canis* specimens of similar size, but is also not very broad or rounded. Based on this parameter no conclusion can be drawn about the identity of specimen 2104.

#### Specimens 667, 1683, 2103, 2329, 2620, 3293 and NMR90

These seven fossil specimens have a (very) thin, distinct anterior border of the coronoid process compared to the rest of their mandible that resembles the typical *Canis* border. This is a very strong indication that these specimens belong to the genus *Canis* and not to *Cuon alpinus*, since such anterior borders are never observed in *Cuon alpinus*.

## 5.4.4 Angular process

### 5.4.4.1 Comparative material

For the results that are discussed see 4.3.5.1. It was observed that in all *Cuon alpinus* specimens (except one) the angular process continues in a crest and in all *Canis* specimens (except one *C. l. familiaris* specimen and two *C. l. lupus* specimens) the crest is either absent or less marked. Continuation of the angular process in a crest is thus typical for *Cuon* and absence of a crest typical for *Canis*, but due to these four exceptional specimens in the comparative material the evidence from the appearance of the angular process is not entirely solid. Based on the observation of either of these typical appearances we cannot entirely exclude the other genus as possible identity; we can only conclude that a fossil specimen with a typical *Canis* appearance is much more likely a *Canis* specimen than *Cuon*. Moreover, there are no major differences between the two *Canis* species, thus we can only identify the fossil North Sea specimens on genus level. One could argue that a fossil specimen in which the process continues in a crest is probably *Cuon alpinus*, unlikely *C. l. lupus*, but even much less probably *C. l. familiaris*, because the only *C. l. familiaris* specimen in which the angular process continues in a crest is a recent specimen from Suriname and not a fossil specimen from the Netherlands. This could mean that this unusual appearance of the angular process in this comparative specimen is due to temporal and/or geographical variation instead of intraspecific variation. But it is not relevant to elaborate further on this topic, since all fossil North Sea specimens for which this parameter could be taken did not have crest.

#### 5.4.4.2 Fossil North Sea material

Only for specimens 535, 667, 2103, 2104, 2329, NMR89 and NMR90 the appearance of the angular process could be determined and all of these seven fossil North Sea specimens had the typical *Canis* appearance: the process was small and not distinct in some specimens and entirely absent in others (4.3.5.2). This means that based on this parameter these seven specimens are much more likely *Canis* specimens than *Cuon* and, although a *Cuon* identity cannot be entirely excluded, the possibility that these specimens are *Cuon* is very small.

### 5.4.5 Relation angular process - mandibular condyle (line k)

#### 5.4.5.1 Comparative material

There are only three fossil North Sea specimens that can be identified with this parameter and results are quite conclusive, thus interpretation of the results (as presented in 4.3.6.1) will be kept brief. We observed that in all comparative *Cuon* specimens the angular process is larger in the aboral direction than the mandibular condyle. This means that when in a fossil specimen the two protuberances are equal in size or when the mandibular condyle is larger than the angular process, the fossil specimen certainly is not *Cuon*. Remaining results indicated that there are some differences between *C. l. lupus* and *C. l. familiaris*, but these are not significant; all three relations between the angular process and mandibular condyle are observed in a significant amount of specimens in both *Canis* species, thus neither species can be entirely excluded as possible identity. Based on this parameter one cannot distinguish between *C. l. familiaris* and *C. l. lupus*. The different trends observed in the recent *C. l. familiaris* specimens from Suriname and the fossil specimens from the Netherlands could be explained by the temporal and/or spatial variable. What the observation of an angular process that is larger than the condyle means is not relevant, since this option was not encountered in the fossil North Sea specimens.

#### 5.4.5.2 Fossil North Sea material

The only three fossil North Sea specimen, for which the relation between the angular process and the mandibular condyle could be determined, had a process and condyle that are equal in size (specimens 2103 and 2104) or a condyle that is larger in the aboral direction than the process (specimen 2329) (4.3.6.2). These three specimens are thus certainly not *Cuon alpinus*, but it cannot be established (based on this parameter) whether these specimens are *C. l. familiaris* or *C. l. lupus*.

### 5.4.6 Conclusions section 'Ramus'

In this paragraph conclusions about the identity of the 13 fossil North Sea specimens will be drawn, based on the combined conclusions of the individual parameters that were presented in the 'Ramus' section. For an overview of all results and interpretation thereof, see appendix XII.

#### Specimen 534 (*C. l. lupus*)

Specimen 534 was measured for 4 of the 6 parameters in the 'Ramus' section (table XII.1). The parameter 'Anterior border of the coronoid process' was entirely inconclusive about the identity of specimen 534 and the parameter 'Aboral border of the ramus' only identified 534 on genus level: 534 is more likely *Canis* than *Cuon*. The parameters 'Distance' *a-d* and *e-e*' were estimated based on a comparative *C. l. lupus* specimen and are thus slightly less solid evidence as parameters that were directly measured on the specimen, but we can still conclude that specimen 534 is not *Cuon alpinus* (based on both distances) and not *C. l. familiaris* (based on distance *a-d*). This section thus confirms with a 97.7% confidence interval the conclusions of the previous two sections: specimen 534 is *C. l. lupus*.

#### Specimen 535 (*Canis*)

Specimen 535 was only measured for the parameter 'Angular process' in this section (table XII.1). Based on this parameter we can only identify specimen 535 on genus level: 535 is more likely *Canis* than *Cuon*. This confirms the conclusions of the previous two sections, but is less conclusive, because the 'Mandible length' section indicated that specimen 535 can be assigned to *C. l. lupus* with a 97.7% confidence interval.

#### Specimen 667 (*Canis*)

Specimen 667 was measured for all parameters in the 'Ramus' section, except 'line k' (table XII.2). All parameters left open the possibility of either of the two *Canis* subspecies as identity for fossil specimen 667. A *Cuon alpinus* identity was only excluded based on qualitative parameters ('Aboral border of the ramus', 'Anterior border of the coronoid process' and 'Angular process') and thus not with a 97.7% confidence interval, but with only an indication of 'not likely *Cuon*/less likely *Cuon* than *Canis*'. Evidence of this section

is thus not very solid for this specimen, on the contrary to the previous two sections in which specimen 667 could be assigned to *C. l. lupus* with a 97.7% confidence interval.

#### **Specimen 1683 (*Canis*)**

This fossil specimen was only measured for one parameter ('Anterior border of the coronoid process') in this section (table XII.2). This parameter only identified specimen 1683 on genus level: 1683 is probably *Canis* and not *Cuon*. Evidence in this section is thus far from conclusive, on the contrary to the previous two sections in which specimen 1683 could be assigned to *C. l. lupus* with a 97.7% confidence interval.

#### **Specimen 2103 (*Canis*)**

Specimen 2103 was measured for all parameters in the 'Ramus' section (table XII.3). Based on the four qualitative parameters in this section ('Aboral border of the ramus', 'Anterior border of the coronoid process', 'Angular process' and 'line k') it can be concluded that specimen 2103 is probably not *Cuon alpinus*, but *Canis*. The two quantitative parameters (that have a statistical confidence interval) were entirely inconclusive. All parameters left open the possibility of either of the two *Canis* subspecies as identity for specimen 2103. Evidence in this section is thus not very conclusive, as was the second section, on the contrary to the first section in which was concluded with a 97.7% confidence interval that specimen 2103 is a *C. l. familiaris* specimen.

#### **Specimen 2104 (*Canis*)**

Specimen 2104 was measured for all parameters in the 'Ramus' section, except the 'Anterior border of the coronoid process' (table XII.3). Based on the three remaining qualitative parameters in this section ('Aboral border of the ramus', 'Angular process' and 'line k') it can be concluded that specimen 2103 is probably not *Cuon alpinus*, but *Canis*. Also for this specimen all parameters left open the possibility of either of the two *Canis* subspecies as identity for 2104. Based on the combined evidence of this third section the identity of specimen 2104 can thus only be established on genus level (2104 is probably not a *Cuon* specimen, but *Canis*), as was also the case in the second section, but on the contrary to the first section in which was concluded with a 97.7% confidence interval that specimen 2104 belongs to the subspecies *C. l. familiaris*.

#### **Specimen 2196 (*C. l. lupus*)**

Specimen 2196 was only measured for the two quantitative parameters in the 'Ramus' section, 'Distance' *a-d* and *e-e'* (table XII.4). Both parameters indicate that specimen 2196 is a *C. l. lupus* specimen with a 97.7% confidence interval. Although the values for these parameters were estimated (based on a comparative *C. l. lupus* specimen), the statistical confidence of this conclusion is not less than when the actual values for these parameters could have been measured, because the specimen ranges of 2196 even fall partially above the *C. l. lupus* population ranges for these parameters. This means that 'Distance' *a-d* and *e-e'* of 2196 are much larger than *C. l. familiaris* and *Cuon alpinus* and that it is very likely that the actual values also would have fallen above the ranges of these two (sub)species. We can thus conclude based on all combined evidence of this section and with a 97.7% confidence interval that specimen 2196 is a *C. l. lupus* specimen, as was concluded for the previous two sections.

#### **Specimen 2329 (*C. l. lupus*)**

Specimen 2329 was measured for all parameters in the 'Ramus' section (table XII.4). Based on the 4 qualitative parameters of this section we could conclude that specimen 2329 is probably not a *Cuon alpinus* specimen, but either of the two *Canis* subspecies. The two quantitative parameters (distances *a-d* and *e-e'*) excluded both *Cuon alpinus* and *C. l. familiaris* as possible identity for specimen 2329 with a 97.7% confidence interval. We can conclude based on the combined evidence of all parameters in this section that specimen 2329 can be assigned to *C. l. lupus* with a 97.7% confidence interval, which confirms the conclusions obtained in the first and second sections.

#### **Specimen 2620 (*Canis*)**

Specimen 2620 was only measured for one parameter ('Anterior border of the coronoid process') in this section (table XII.5). This parameter left open the possibility of either of the two *Canis* subspecies as identity for specimen 2620 and indicated that 2620 is probably not *Cuon alpinus*. Evidence in this section is thus sparse and far from conclusive, on the contrary to the first and second sections in which was concluded with a 97.7% confidence interval that specimen 2620 is a *C. l. lupus* specimen.

#### **Specimen 3219 (*Canis*)**

Specimen 3219 could not be measured for any of the parameters in the 'Ramus' section (table XII.5). Since the previous two sections only indicated on genus level that 3219 is not *Cuon*, but *Canis*, there is still no solid evidence for the identity of specimen 3219 on subspecies level.

**Specimen 3293 (*Canis*)**

Specimen 3293 could only be measured for the parameter 'Anterior border of the coronoid process' in this section (table XII.6). This parameter left open the possibility of either of the two *Canis* subspecies as identity for 3293. Evidence in this section is thus sparse and far from conclusive, on the contrary to the first section in which was concluded with a 97.7% confidence interval that this fossil North Sea specimen belongs to the subspecies *C. l. lupus*.

**Specimen NMR89 (*Canis*)**

NMR89 was only measured for the 'Angular process' in this section (table XII.6), but evidence of this parameter was far from conclusive and only indicated that NMR89 is more likely a *Canis* specimen than a *Cuon* specimen. This confirms the conclusion of the previous two sections that NMR89 is not *Cuon alpinus*, but does not aid in the identification of this specimen, since the previous two sections contradicted each other: the 'Mandible length' section indicated with a 97.7% confidence interval that NMR89 is *C. l. lupus*, but and the 'Mandible (width, height and ratios)' section indicated with a 97.7% confidence interval that NMR89 is *C. l. familiaris*.

**Specimen NMR90 (*Canis*)**

NMR90 was measured for 4 parameters in the 'Ramus' section ('Distance' *a-d* and *e-e'*, 'Anterior border of the coronoid process' and the 'Angular process', table XII.7). All parameters left open the possibility of either of the two *Canis* subspecies as identity for NMR90. *Cuon alpinus* was excluded by one quantitative parameter ('Distance' *e-e'*) and the two qualitative parameters. Keeping in mind that the value of *e-e'* was estimated for this specimen (based on a comparative *C. l. familiaris* specimen), we can conclude (with a 97.7% confidence interval) that NMR90 is not *Cuon alpinus*. This confirms the conclusion of the first section, but is less conclusive, because the first section also excluded *C. l. lupus* as possible identity for NMR90.

## 5.5 Teeth

### 5.5.1 Dental formula

#### 5.5.1.1 Comparative material

The typical dental formula of Canidae is 3/3-1/1-4/4-2/3, but the unique dentition of *Cuon* within the Canidae family is 3/3-1/1-4/4-2/2 (Durbin et al., 2008). Literature already indicated that variation in the dental formula of Canidae is possible and results of the comparative dataset used in this study confirm that the dental formula of *C. l. familiaris* specimens indeed can vary. All *Cuon* and *C. l. lupus* specimens on the other hand had the typical dentition of their genus (4.4.1.1). Abnormalities observed in the dentition of *C. l. familiaris* varied from extra teeth to missing teeth (appendix XI), but the two specimens with an atypical dentition that are relevant for this study are the two comparative *C. l. familiaris* specimens in which an  $M_3$  is missing. As a result the mandibular dental formula of these two specimens is 3-1-4-2, which is the same as the *Cuon* mandibular dental formula. Although this dental formula always occurs in *Cuon* and only very rarely in *C. l. familiaris* (4.4.1.1), taxonomic assignment of a specimen to *Cuon* or *C. l. familiaris* solely based on this mandibular dental formula is not possible, because the presence of only two molars can occur in *Cuon* as well as in *C. l. familiaris* specimens (assuming that these comparative *C. l. familiaris* specimens were classified correctly). If a maxillary dental formula also is known, the combination of the two dental formulas could possibly give more conclusive evidence (since a maxillary dentition of 3-1-4-1 only occurs in Canidae (Thenius, 1989)), but this cannot be applied in this study, since we only have mandibles. We also observed that in these two fossil *C. l. familiaris* specimens the dental formula was not the only 'typical *Cuon*' result that was observed; these two *C. l. familiaris* specimens show a combination of typical *Canis* and *Cuon* values for several parameters (appendices XII and XIII). They are thus nice examples of nature's variation and continuum: there is no distinct separation between species and classification based on supposed typical characteristics is often less reliable and simple as it would seem. Classification becomes even harder when interbreeding occurs between *Canis* subspecies.

In summary, based on the mandibular dental formula we can draw the following conclusions:

When the dental formula is 3-1-4-2, the fossil specimen can very well be *Cuon alpinus*, possibly also *C. l. familiaris*, but not *C. l. lupus*. When the dental formula is 3-1-4-3, the fossil specimen is certainly a *Canis* specimen, and certainly not *Cuon alpinus*.

#### 5.5.1.2 Fossil North Sea material

Specimens 534, 535, 667, 1683, 2103, 2104, 2196, 2329, 2620, 3293 and NMR89 have the typical Canidae dental formula and can thus be assigned to the genus *Canis* (plate 4.1). These eleven fossil North Sea specimens are certainly not *Cuon alpinus*. For specimen 3219 the dental formula could not be determined, thus no indication for the identity of 3219 can be given based on this parameter. The most interesting specimen is NMR90, which has a mandibular dental formula of 3-1-4-2. Based on this missing  $M_3$  and measurements of molars, this specimen was suspected to be *Cuon alpinus*, but we know now that this dental formula can also be observed in *C. l. familiaris* specimens. Since *C. l. familiaris* and *C. l. lupus* belong to the same genus one could suspect that similar variation in the dental formula of *C. l. lupus* is also possible and that this was not observed in this comparative dataset due to the quite small sample size for *C. l. lupus*. But we can reasonably assume that NMR90 is not likely *C. l. lupus*, because several previous parameters already indicated that NMR90 is too small for *C. l. lupus*. Based on its dental formula NMR90 is likely *Cuon alpinus*, but *C. l. familiaris* cannot be excluded.

### 5.5.2 Height of the crown of $P_4$ and $M_1$

Since the heights of the crowns of  $P_4$  and  $M_1$  have similar results (4.4.2), they will be interpreted together: if is not explicitly stated otherwise, in each paragraph conclusions hold true for both parameters. Only where the parameters do not have the same results, results will be mentioned separately.

#### 5.5.2.1 Comparative material

For all results, see 4.4.2.2a. Results of the peculiar standard deviation versus sample size and the difference between the fossil *C. l. familiaris* specimens from the Netherlands and the recent specimens from Suriname are as expected and were interpreted for all parameters in 5.1.3. Results of the mean values and ranges of *Cuon alpinus* as compared to *Canis* are different from results for previous parameters: for this parameter the *Cuon alpinus* mean is on average slightly larger than the *C. l. familiaris* mean and the *C. l. lupus* data cloud has shifted with respect to *C. l. familiaris* and *Cuon alpinus*. For the height of the crown *C. l. lupus* still has on average the largest absolute values and *C. l. familiaris* and *Cuon alpinus* have lower and similar crown

heights, as in previous parameters, but it was observed that *C. l. lupus* has lower premolar crown heights in proportion to its molar crown height compared to both *Cuon alpinus* and *C. l. familiaris*, while based on literature it was expected that in *Cuon alpinus* specimens the premolars have relatively higher crowns than in both *Canis* species (García and Arsuaga (1998) int. al.). For this parameter *C. l. familiaris* is thus not only more similar to *Cuon alpinus* than to *C. l. lupus* in general size interval (as was the case in previous parameters), but also in the premolar to molar crown height ratio. Although *Cuon alpinus* values are on average slightly higher than *C. l. familiaris* values (in most parameters the reversed trend is observed) both species occupy a similar size interval. There are thus no major differences between *Cuon alpinus* and *C. l. familiaris* and one cannot distinguish between these two species based on this parameter. On the contrary, *C. l. lupus* is not only larger than *C. l. familiaris* and *Cuon alpinus* for this parameter, but also has another premolar to molar crown height ratio. The relative height of the crown of  $P_4$  turned out not to be a characteristic to distinguish *Cuon alpinus* from *Canis*, but *C. l. lupus* from *C. l. familiaris* and *Cuon alpinus*. This parameter is another example in which the difference between genera and species is not as solid as expected: sometimes there are more similarities between two species of two different genera than between two species within a genus and a large comparative dataset is necessary to verify whether a differentiating characteristic is sufficiently solid to use in the identification of specimens.

### 5.5.2.2 Fossil North Sea material

All results that are discussed in this paragraph can be found in 4.4.2.2b.

#### Specimen 535

This specimen is almost certainly a *C. l. lupus* specimen: the specimen range of 535 falls entirely outside the sample and population ranges of *C. l. familiaris* and *Cuon alpinus*, which means that 97.7% of the specimens of the entire natural population of *C. l. familiaris* and *Cuon alpinus* have lower crowns than specimen 535. There is only a 2.3% chance that 535 is one of these species (although this chance is small, keep in mind that based on solely this parameter the possibility still exists that 535 is a *C. l. familiaris* or *Cuon alpinus* specimen with extremely high crowns). The mean value of 535 is most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *Cuon alpinus* and *C. l. familiaris* specimens, which circumstantially supports the conclusion that 535 is *C. l. lupus*. This specimen only had an  $M_1$ , thus no results are known about the crown height of its  $M_1$  in proportion to its  $P_4$ .

#### Specimens 667, 2103, 2104 and NMR90

The specimen ranges of these four fossil North Sea specimens fall in the sample and population ranges of all three comparative species. Even if specimens 667 and NMR90 in reality had slightly higher crowns (values were estimated), they would still fall within all comparative ranges, because overlap between the ranges is not just marginally. This means that the four specimens could be either *Cuon alpinus* or *Canis*. Mean values of specimens 667 and NMR90 are not indicative for the identity of these specimens. For specimens 2103 and 2104 they indicated that these two specimens are more similar to the average *Cuon alpinus* specimen, but this is just a circumstantial indication. Neither of the specimens has a particularly high crown of its  $M_1$  in proportion to its  $P_4$  crown height compared to other *C. l. familiaris* and *Cuon alpinus* specimens, thus the proportional crown heights of  $P_4$  and  $M_1$  are neither informative. The identity of specimens 667, 2103, 2104 and NMR90 cannot be determined based on the crown heights.

#### Specimen 1683

Specimen 1683 falls entirely outside the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* and falls partly outside (above) the *C. l. lupus* sample range for  $M_1$ , which means that there is only a 2.3% chance that 1683 is *Cuon alpinus* or *C. l. familiaris* and very probably is *C. l. lupus*. The crown heights of this specimen were 'lower boundary' estimates, which means that the exact crown height for  $P_4$  and  $M_1$  was certainly not lower and possibly even larger. Specimen 1683 has thus quite large crowns and the  $P_4$  is quite low in proportion to the crown height of  $M_1$  in comparison to *Cuon alpinus* and *C. l. familiaris* specimens, which is typical for *C. l. lupus*. All evidence supports the conclusion that specimen 1683 is *C. l. lupus*.

#### Specimen 2196

Specimen 2196 is almost certainly a *C. l. lupus* specimen based on its crown height. The specimen range of 2329 falls entirely outside (above) the sample and population ranges of *Cuon alpinus* and *C. l. familiaris*, thus there is only 2.3% chance that 2196 is *Cuon alpinus* or *C. l. familiaris*. Values for the  $M_1$  were estimated, but particularly for the  $M_1$  the minimum of the specimen range of 2196 is much larger than the *C. l. familiaris* and *Cuon alpinus* maxima. Moreover, the estimated values indicate that the actual height of the crown of the  $M_1$  certainly was not lower and possibly even larger. Mean values confirm that 2196 is most similar to the average *C. l. lupus* specimen and specimen 2196 is positioned above the *C. l. lupus* trend line, which means that in this specimen the height of the crown of  $M_1$  is clearly larger in proportion to its  $P_4$  crown, as is typical in *C. l. lupus*. All evidence supports the conclusion that specimen 2196 is *C. l. lupus*.

### **Specimen 2329**

In this specimen the values for both  $P_4$  and  $M_1$  were estimated and thus possibly larger, but even the estimated values already fall entirely outside (above) the sample and population ranges of *Cuon alpinus* and *C. l. familiaris*. Specimen 2329 is thus almost certainly *C. l. lupus*; there is only a 2.3% chance that this specimen belongs to *C. l. familiaris* or *Cuon alpinus*. The facts that 2329 is most similar to the average *C. l. lupus* specimen and that the height of the crown of  $M_1$  is proportionally larger than the crown height of  $P_4$  compared to *Cuon alpinus* and *C. l. familiaris* specimens, confirms that 2329 is *C. l. lupus*.

### **Specimen 3219**

For this specimen the values for both teeth were estimated. The specimen range of 3219 falls within the sample and population ranges of all three comparative species for  $P_4$ , but even if the actual crown heights had been slightly larger the specimen range of 3219 would still overlap with all three comparative ranges. Based on  $P_4$  the identity of 3219 can thus not be established. For  $M_1$  the overlap of 3219 with the sample ranges of *C. l. familiaris* and *Cuon alpinus* is only very small, thus it is very likely that the actual crown height of  $M_1$  would fall outside these two ranges. Moreover, 3219 falls outside the population ranges of these two species, which means that there is only a 2.3% chance that 3219 is *C. l. familiaris* or *Cuon alpinus*. Mean values and the relative  $P_4$  crown height in proportion to the molar crown height are not indicative for a species in this specimen, but based on the  $M_1$  population ranges we can conclude that specimen 3219 is very likely a *C. l. lupus* specimen.

### **Specimen 3293**

Also this specimen is almost certainly a *C. l. lupus* based on its crown heights: 3293 falls entirely outside (far above) the sample and population ranges of *Cuon alpinus* and *C. l. familiaris*, thus there is only a 2.3% chance that this specimen is *C. l. familiaris* or *Cuon alpinus* (moreover, because the crown height of  $P_4$  was estimated and thus possibly higher than the value that was used to estimate the specimen range). Specimen 3293 does not have a particular high molar crown in proportion to its fourth premolar crown, but mean values circumstantially support the conclusion that 3293 is *C. l. lupus*.

## **5.5.3 Length and breadth of $M_1$ and $M_2$**

Since the length and breadth of the molars have similar results (4.4.3.1a and 4.4.3.2a), these two dimensions of the molars will be interpreted together: if is not explicitly stated otherwise, in each paragraph conclusions hold true for both parameters. Only where the parameters do not have the same results, results will be mentioned separately. Everything that could be interpreted about the comparative material was already done for previous parameters (see previous paragraphs and mainly 5.2.1.1). Results of the comparative material for the length and breadth of the two molars are as expected (thus similar to previous parameters): there are no remarkable observations. There is no need to interpret the comparative material for these parameters separately.

### **5.5.3.1 Length and breadth of $M_1$**

All results that are discussed in this paragraph can be found in 4.4.3.1b.

#### **Specimens 535, 1683, 2196, 2620 and 3293**

As already could be seen in fig. 4.30 these five specimens all plot in the upper part of the *C. l. lupus* range and belong almost certainly to this species. The specimen ranges of these four fossil North Sea specimens fall entirely outside (far above) the sample and population ranges of *C. l. familiaris* and *Cuon alpinus* and within the *C. l. lupus* ranges. Specimen 1683 even falls partly outside (above) the *C. l. lupus* sample range for the breadth of  $M_1$ . This means that the  $M_1$  of 97.7% of all *C. l. familiaris* and *Cuon alpinus* specimens of their entire natural population is smaller and shorter than the first molars of these five specimens. There is only a 2.3% chance that these specimens are *C. l. familiaris* or *Cuon alpinus*. The mean values of these specimens all were most similar to the average *C. l. lupus* specimen and much less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens, which circumstantially supports the conclusion that specimens 535, 1683, 2196, 2620 and 3293 are *C. l. lupus*.

#### **Specimen 667**

Results for this specimen are less conclusive: 667 falls within the *C. l. familiaris* and *Cuon alpinus* sample and population ranges for the length and breadth of  $M_2$ . Although overlap with the *Cuon alpinus* population range for the breadth is only partial, *Cuon alpinus* cannot be excluded as possibility; specimen 667 can either be *C. l. familiaris* or *Cuon alpinus*. Specimen 667 falls entirely outside the *C. l. lupus* population ranges for both the length and breadth of  $M_1$ , based on which we can conclude that 667 is almost certainly not this species. Mean values indicate that 667 is most similar to the average *C. l. familiaris* specimen, slightly less



similar to the average *Cuon alpinus* specimen and most dissimilar to the average *C. l. lupus* specimen, which circumstantially supports the conclusion that specimen 667 is not *C. l. lupus*, but can either be *C. l. familiaris* or *Cuon alpinus*.

### Specimen 2103

Specimen 2103 falls entirely within the *C. l. familiaris* sample and population ranges for both the length and breadth of  $M_1$  and within many *C. l. lupus* and *Cuon alpinus* ranges, based on which 2103 could still be one of all three comparative species. Only the *C. l. lupus* and *Cuon alpinus* population ranges for the breadth of  $M_1$  give more conclusive evidence: 2103 falls entirely outside these ranges, thus there is only a 2.3% chance that 2103 is *C. l. lupus* or *Cuon alpinus*. Mean values (2103 is most similar to the average *C. l. familiaris* specimen) support the conclusion that 2103 is *C. l. familiaris*.

### Specimen 2104

This fossil specimen had only values for the length of  $M_1$ . The specimen ranges falls entirely within the *Cuon alpinus* and *C. l. familiaris* sample and population ranges and partly inside the *C. l. lupus* sample range, but entirely outside (below) the *C. l. lupus* population range for the length of  $M_1$ . This means that 97.7% of the *C. l. lupus* specimens of the entire natural population has a longer first molar than 2104; there is only a 2.3% chance that specimen 2104 is *C. l. lupus*, but based on the dimensions of its  $M_1$  2104 could still either be *Cuon alpinus* or *C. l. familiaris*. Mean values indicate that specimen 2104 is most dissimilar to the average *C. l. lupus* specimen and most similar to *C. l. familiaris*, which supports the conclusion that 2104 is not *C. l. lupus*, but based on which cannot be concluded that 2104 is *C. l. familiaris* (evidence is too circumstantial).

### Specimen 2329

Specimen 2329 falls entirely within the *C. l. lupus* sample and population ranges and entirely outside (above) the *Cuon alpinus* sample and population ranges for both the length and breadth, which means that 2329 can be *C. l. lupus*, but almost certainly is not *Cuon alpinus*, because 97.7% of the *Cuon alpinus* specimens of the entire natural population have larger  $M_1$  than 2329. *C. l. familiaris* can also be excluded as possible identity for this fossil specimen, but only based on the length of  $M_1$ : 2329 falls entirely outside (above) the sample and population ranges of *C. l. familiaris* for the length, thus there is only a 2.3% chance that 2329 is *C. l. familiaris*. The evidence that 2329 is not *Cuon alpinus* is slightly more solid than the evidence that 2329 is not *C. l. familiaris*, because two parameters (length and breadth) indicated that 2329 is not *Cuon alpinus*, whereas only one parameter (length) indicated that 2329 is not *C. l. familiaris*. That specimen 2329 almost certainly is *C. l. lupus* could already be guessed from the position of 2329 in the upper part of fig. 4.30 and the fact that the mean value of specimen 2329 is most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens.

### Specimen 3219

Specimen 3219 falls entirely within the *C. l. familiaris* sample and population ranges for both the length and breadth of  $M_1$  and partly within some *C. l. lupus* and *Cuon alpinus* sample and population ranges for the length and breadth. Although these partial overlaps indicate that 3219 is quite small respectively large compared to all comparative *C. l. lupus* and *Cuon alpinus* specimens, specimen 3219 could still be one of these two species. Only the *C. l. lupus* and *Cuon alpinus* population ranges for the breadth of  $M_1$  give more conclusive evidence: 3219 falls entirely outside these ranges, which means that there is only a 2.3% chance that 2103 is *C. l. lupus* or *Cuon alpinus*. Mean values, which indicate that 3219 is most similar to *C. l. familiaris*, circumstantially support the conclusion that specimen 3219 is *C. l. familiaris*.

### Specimen NMR90

NMR90 falls partially within the *C. l. lupus* sample ranges for the length and breadth, but entirely outside corresponding population ranges, based on which we can conclude that there is only a 2.3% chance that specimen NMR90 is *C. l. lupus*. NMR90 falls within the *C. l. familiaris* and *Cuon alpinus* sample and population ranges (although only partly within the *Cuon alpinus* population range for the length), based on which one cannot conclude whether NMR90 is *Cuon alpinus* or *C. l. familiaris*. Mean values circumstantially support the conclusion that NMR90 is not *C. l. lupus* (the NMR90 mean is most dissimilar to the average *C. l. lupus* specimen), but the fact that NMR90 is most similar to the average *C. l. familiaris* specimen and less similar to the average *Cuon alpinus* specimen cannot be used as solid evidence for the identification of NMR90. Based on the dimensions of  $M_1$  NMR90 can be either *C. l. familiaris* or *Cuon alpinus*.

### Values from literature

For the length and breadth of  $M_1$  values of respectively 28 and 23 *Cuon alpinus* specimens from literature were added to the comparative dataset and the fossil North Sea specimens were compared to the newly calculated sample and population ranges (table IX.5, IX.6 and appendix XII).

*Following interpretations discuss the results of the length of  $M_1$*

For specimens 535, 667, 1683, 2104, 2196, 2329, 2620 and 3293 the results and thus interpretations obtained by the comparison to the new comparative ranges confirm previous conclusions. Specimens 667 and 2104 still fall entirely within both the *Cuon alpinus* sample and population ranges, which means that these specimens indeed still can belong to the *Cuon* genus. Specimens 535, 1683, 2196, 2329, 2620 and 3293 still fall entirely outside the *Cuon alpinus* sample and population ranges, which means that the extended dataset confirms that it is very unlikely that these specimens are *Cuon alpinus* (for which there is only a 2.3% chance). Specimens 2103 and 3219 originally fell partly outside both *Cuon alpinus* ranges, but fall entirely within both new ranges, which confirms the previous conclusion that it is still possible that these specimens are *Cuon alpinus*. Specimen NMR90 originally fell within the *Cuon alpinus* sample range and partly outside corresponding population range, but falls entirely within both new ranges. This means that also this specimen still can be *Cuon alpinus* based on the length of its  $M_1$ .

*Following interpretations discuss the results of the breadth of  $M_1$*

For specimens 535, 1683, 2196, 2620, 3293 and NMR90 the results and thus interpretations obtained by the comparison to the new comparative ranges confirm previous conclusions. Specimen NMR90 still falls entirely within the *Cuon alpinus* sample and population ranges, which means that also based on the extended dataset *Cuon alpinus* cannot be excluded as possible identity for specimen NMR90. Specimens 535, 1683, 2196, 2620 and 3293 still fall entirely outside both *Cuon alpinus* ranges, thus the extended dataset confirms that it is very unlikely that these specimens are *Cuon alpinus* (for which there is only a 2.3% chance). Specimen 667 originally fell within the *Cuon alpinus* sample range and partly outside the population range, but falls entirely within both new *Cuon alpinus* ranges. This confirms that partial overlaps do not reduce the chance that a specimen is that species and that specimen 667 can still be *Cuon alpinus*. Specimens 2103 and 3219 fell originally partly outside the *Cuon alpinus* sample range and entirely outside corresponding population range, but fall entirely within both *Cuon alpinus* ranges for the new extended dataset. This means that based on the extended dataset specimens 2103 and 3219 very well can be *Cuon alpinus* and that this chance is not only 2.3% as was previously concluded. Specimen 2329 originally fell outside the *Cuon alpinus* sample and population ranges, but falls only partly outside the new *Cuon alpinus* population range, which means that based on the new dataset cannot be concluded that there is only a 2.3% chance that this specimen is *Cuon alpinus*; *Cuon alpinus* cannot be entirely excluded as possible identity for specimen 2329.

### **5.5.3.2 Length and breadth of $M_2$**

All results that are discussed in this paragraph can be found in 4.4.3.2b.

#### **Specimens 534 and 535**

These two specimens both fall entirely outside (above) all sample and population ranges of *Cuon alpinus* and *C. l. familiaris* (except the *C. l. familiaris* sample range for the length of  $M_2$  for which there is partial overlap). This means that 97.7% of the *Cuon alpinus* and *C. l. familiaris* specimens of their entire natural population have smaller dimensions of the  $M_2$  than these two fossil North Sea specimens. Both specimens fall within all *C. l. lupus* ranges and belong almost certainly to this species. Mean values (534 and 535 are most similar to the average *C. l. lupus* specimen and much more dissimilar to the average *C. l. familiaris* and *Cuon alpinus* specimens) support this conclusion.

#### **Specimen 667**

Specimen 667 falls (partially) in all ranges of all comparative material except the *C. l. lupus* sample and population ranges for the breadth and the *Cuon alpinus* population range for the length. Based on the breadth of  $M_2$  *C. l. lupus* can thus be excluded as possibility and based on the length *Cuon alpinus* can be excluded as possible identity for 667: there is only a 2.3% chance that specimen 667 is *C. l. lupus* or *Cuon alpinus*. Mean values circumstantially support the conclusion that 667 is *C. l. familiaris*: 667 is most similar to the average *C. l. familiaris* specimen and less similar to the average *Cuon alpinus* and *C. l. lupus* specimens for both the length and breadth of  $M_2$ .

#### **Specimens 1683 and 2620**

These two specimens have similar results that lead to the same conclusion: 1683 and 2620 are *C. l. lupus* specimens. Both specimens fall entirely within the *C. l. lupus* sample and population ranges for the breadth of  $M_2$ , entirely outside the *C. l. familiaris* sample and population ranges for the breadth and entirely outside the *Cuon alpinus* sample and population ranges for the length and breadth. This means that there is only a 2.3% chance that these specimens are *C. l. familiaris* or *Cuon alpinus* and they can already be assigned to *C. l. lupus*. For specimen 1683 this is the only evidence for a *C. l. lupus* identity, because the specimen range of 1683 still partially overlapped with both the sample and population range of *C. l. familiaris* for the length, which means that solely based on the length of  $M_2$  1683 also could have been *C. l. familiaris*. For

specimen 2620 the *Canis* ranges only confirmed the *C. l. lupus* identity: the specimen range of 2620 fell outside these ranges for the length. This seems contradictory, because this means that for the length of  $M_2$  there is only a 2.3% chance that 2620 is *C. l. lupus*, while we already concluded based on the breadth that 2620 is almost certainly *C. l. lupus*. Since specimen 2620 is most similar to the average *C. l. lupus* specimen, plots in the upper part of fig. 4.30, is much more dissimilar to the average *Cuon alpinus* and *C. l. familiaris* specimens and has to be one of the three comparative species, the most logical explanation for the high value of the length of  $M_2$  compared to all comparative *C. l. lupus* specimens is, that 2620 is a *C. l. lupus* specimen with an extremely long  $M_2$ .

#### **Specimen 2104**

Specimen 2104 falls entirely within the *C. l. familiaris* sample and population ranges for both the length and breadth of  $M_2$  and entirely outside (below) the *C. l. lupus* sample and population ranges for the breadth, which means that 2104 could very well be a *C. l. familiaris* specimen, but is almost certainly not *C. l. lupus* (there is only a 2.3% chance that 2104 is this species). This fossil specimen partially overlaps with the upper part of all *Cuon alpinus* ranges, which is an indication that 2104 is quite large for a *Cuon alpinus* specimen, but still could be this species. Mean values indicate that 2104 is most similar to the average *C. l. familiaris* specimen and less similar to the average *Cuon alpinus* specimen. Although the marginal overlap and the means are slight indicators that 2104 is more similar to *C. l. familiaris* than to *Cuon alpinus*, *Cuon alpinus* cannot be excluded as possibility. Specimen 2104 is thus almost certainly not *C. l. lupus*, but can either be *C. l. familiaris* or *Cuon alpinus*.

#### **Specimen 2196**

Specimen 2196 is almost certainly not a *C. l. familiaris* or *Cuon alpinus* specimen: the specimen range of 2196 falls outside all ranges of these two species (although only partially for the *C. l. familiaris* sample range for the length), thus 97.7% of the *C. l. familiaris* and *Cuon alpinus* specimens have shorter and smaller  $M_2$  than 2196. The  $M_2$  of 2196 even has quite large dimensions for a *C. l. lupus* specimen: 2196 partially falls above the *C. l. lupus* population range for the length of  $M_2$ . As was already obvious from the position of 2196 in the upper part of fig. 4.30, the mean of specimen 2196 is most similar to the average *C. l. lupus* specimen and much less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens, which circumstantially confirms the conclusion that specimen 2196 is *C. l. lupus*.

#### **Specimen 3293**

This fossil specimen falls entirely outside the *Cuon alpinus* sample and population ranges and within the *C. l. lupus* sample and population ranges for both the length and breadth of  $M_2$ , which means that 3293 could very well be a *C. l. lupus* specimen, but almost certainly is not *Cuon alpinus* (the chance that 3293 is *Cuon alpinus* is only 2.3%). Specimen 3293 partially falls within the *C. l. familiaris* ranges for the breadth, which means that 3293 has a quite broad  $M_2$  for a *C. l. familiaris* specimen, but can still be this species. Fortunately, the specimen range does not overlap with the *C. l. familiaris* population range for the length of  $M_2$ , which means that there is only a 2.3% chance that 3293 is *C. l. familiaris*. The mean value of specimen 3293 is most similar to the average *C. l. lupus* specimen and much less similar to the average *C. l. familiaris* and *Cuon alpinus* specimens, which circumstantially supports the conclusion that 3293 is *C. l. lupus*.

#### **Values from literature**

For the breadth of  $M_2$  values of 16 *Cuon alpinus* specimens from literature were added to the comparative dataset and the fossil North Sea specimens were compared to the newly calculated sample and population ranges (table IX.5, IX.6 and appendix XII).

For specimens 534, 535, 667, 1683, 2196, 2620 and 3293 the results and thus interpretations obtained by the comparison to the new comparative ranges confirm previously made conclusions. Specimen 667 still falls entirely within the *Cuon alpinus* sample and population ranges, which means that it is still possible that this specimen is *Cuon alpinus*. Specimens 534, 535, 1683, 2196, 2620 and 3293 still fall entirely outside both *Cuon alpinus* ranges, thus the extended dataset confirms that it is very unlikely that these specimens are *Cuon alpinus* (for which there is only a 2.3% chance) and probably belong to the *Canis* genus. Only for specimen 2104 results were slightly different, but this does not change the conclusion: the specimen range of 2104 originally fell partially outside both *Cuon alpinus* ranges, based on which a *Cuon alpinus* identity could not be excluded. Specimen 2104 falls entirely within the new *Cuon alpinus* sample and population ranges, which means that based on the extended dataset it is also still possible that specimen 2104 is *Cuon alpinus*.

## 5.5.4 Cusps on molars

### 5.5.4.1 Cusps of M<sub>1</sub>

#### 5.5.4.1a Comparative material

For all results, see 4.4.5.1a. In general one can distinguish between *Canis* and *Cuon* based on the overall appearance of the M<sub>1</sub>: *Cuon* specimens have a smaller M<sub>1</sub> in which the three principal cusps (proto-, para- and hypoconid) are aligned and centered, while in *Canis* specimens the five principal cusps are more positioned on the lingual and buccal sides of the M<sub>1</sub> as a result of which the tooth is broader and possesses a clear talonid and trigonid basin. With respect to the cusps of the M<sub>1</sub>, results of the comparative material indicated that the difference between *Canis* and *Cuon* lies in the meta- and entoconid. In both *Canis* species all five principal cusps (proto-, para-, meta-, hypo- and entoconid) are always present and well individualized, thus one cannot differentiate between *C. l. lupus* and *C. l. familiaris* based on this parameter. In *Cuon* the proto-, para- and hypoconid are also always present, but the meta- and entoconid are often absent. This means that, when in a fossil specimen the meta- or entoconid or both are absent and the three principal cusps are aligned and centered, the specimen can be assigned to *Cuon* with absolute certainty. But when one or both of these cusps are present, a fossil specimen cannot directly be assigned to the genus *Canis*, because a metaconid and entoconid can also be present in *Cuon alpinus* specimens. If more than three cusps are present in the M<sub>1</sub>, the identity of the fossil specimen can be determined based on the appearance of the meta- and entoconid:

We observed that in 33% of the *Cuon alpinus* specimens a metaconid is present, but that in half of these species (15% of all the comparative *Cuon alpinus* specimens) this metaconid is much less individualized than the typical *Canis* metaconid and can clearly be distinguished from a *Canis* metaconid. In the remaining 19% the metaconid was well individualized and identical to a *Canis* metaconid. This means that solely based on the presence and appearance of a metaconid one fifth of the *Cuon alpinus* population cannot be distinguished from *Canis* species. In 15% of the *Cuon alpinus* specimens an entoconid was present additionally to the metaconid, but this entoconid had a totally different appearance than the typical *Canis* entoconid: it was cingulum-like, not well individualized and did not result in a talonid basin. This means that based on the (absence and) appearance of the entoconid it can always be determined whether a specimen belongs to the *Cuon* or *Canis* genus. This also means that the 19% of the *Cuon alpinus* specimens, which possessed a well individualized metaconid, can still be assigned to *Canis* or *Cuon* based on the appearance of their entoconid.

The cusps of the M<sub>1</sub> can give conclusive evidence about the identity of the fossil North Sea specimens: when all five principal cusps are present and well individualized and/or a clear talonid basin is present the specimen can be assigned to *Canis* with absolute certainty and when only three principal cusps are present (aligned and centered) the specimen can be assigned to *Cuon alpinus* with absolute certainty.

#### 5.5.4.1b Fossil North Sea material

For all results discussed below see 4.4.5.1b and plate 4.2.

##### Specimens 535, 667, 1683, 2103, 2196, 2329, 3219 and 3293

The M<sub>1</sub> of some of these 8 fossil North Sea specimens were slightly eroded, but in all molars a high trigonid including a pronounced and well individualized protoconid, paraconid and metaconid and a shorter and smaller talonid including a pronounced and well individualized hypoconid (buccal), entoconid (lingual) and talonid basin could clearly be identified. This means that specimens 535, 667, 1683, 2103, 2196, 2329, 3219 and 3293 are certainly not *Cuon alpinus* specimens, but *Canis* specimens.

##### Specimens 2104 and 2620

The M<sub>1</sub> of these two specimens are considerably eroded and the presence or absence of a metaconid could not be determined. However, these specimens clearly possess a well individualized (para-, proto-,) hypo- and entoconid and a clear talonid basin. A clear talonid basin is only formed when both the hypo- and entoconid are present and well individualized. Since this is only the case in the molars of both *Canis* species, we can conclude that specimens 2104 and 2620 are *Canis* specimens and do certainly not belong to *Cuon alpinus*.

##### Specimen NMR90

In NMR90 only the para- and protoconid could be identified as well individualized cusps, based on which this specimen cannot be assigned to a particular genus. Although the meta-, hypo- and entoconid could not be directly identified on this M<sub>1</sub>, features that are related to these cusps gave an indication for their presence. In

most *Cuon alpinus* specimens the tiny groove that was observed on the labial side of the protoconid of the M<sub>1</sub> in NMR90 is absent, because the protoconid is centered and a metaconid is missing (the metaconid causes this groove in *Canis* species). This is an indication that a metaconid was originally present and that NMR90 is more likely a *Canis* species, because the presence of a metaconid is much more rare in *Cuon alpinus*. Additionally, a clear indentation is present between the distolingual part of the protoconid and the distolingual edge of the talonid. Such an indentation is only seen in *Canis* specimens, where this is caused by the presence of a talonid basin and a lingually positioned entoconid. In all *Cuon alpinus* specimens such an indentation is absent, because the hypoconid is centered in the talonid or the entoconid (if present) is cingulum-like. This is strong evidence for the presence of a well individualized entoconid on the lingual side of the M<sub>1</sub> of NMR90, and thus a *Canis* identity of NMR90. It is thus very probable that in NMR90 originally a metaconid, entoconid and talonid basin were present, which means that NMR90 can be assigned to *Canis*. Although the evidence for the presence of the meta-, hypo- and entoconid is strong, these cusps were not directly observed on the M<sub>1</sub>, thus this conclusion is slightly less conclusive than for the previous specimens in which all cusps were directly observed.

## 5.5.4.2 Cusps of M<sub>2</sub>

### 5.5.4.2a Comparative material

For all results that are discussed, see 4.4.5.2a. In both *Canis* species all four principal cusps of the M<sub>2</sub> (proto-, para-, hypo- and entoconid) are always present and well individualized (except the entoconid, which is mostly cingular in appearance), thus one cannot differentiate between *C. l. lupus* and *C. l. familiaris* based on this parameter. In *Cuon alpinus* the proto- and hypoconid are also always present, but the meta- and entoconid are often absent. This means that, when in a fossil specimen the meta- or entoconid or both are absent and the two principal cusps (proto- and hypoconid) are aligned and centered, the specimen can be assigned to *Cuon alpinus* with absolute certainty. But when one or both of these cusps are present, a fossil specimen cannot directly be assigned to the genus *Canis*, because a metaconid and entoconid can also be present in *Cuon alpinus* specimens (as was the case for the M<sub>1</sub>). If the metaconid and/or entoconid are present in the M<sub>2</sub>, the identity of the fossil specimen can be determined based on the appearance of all cusps:

The protoconid of *Cuon alpinus* specimens is mostly centered in the trigonid (85% of the *Cuon alpinus* specimens), but this was never observed in *Canis* specimens, where the protoconid is always positioned in the mesiobuccal quadrant. A centered protoconid is thus a strong indication for a *Cuon alpinus* identity. But a protoconid that is positioned in the mesiobuccal quadrant was observed in both *Canis* and *Cuon alpinus* specimens. Although this position of the protoconid occurs much less in *Cuon alpinus* than in *Canis*, a fossil specimen in which the protoconid is not centered can still be either *Canis* or *Cuon alpinus* and the identity has to be determined from the remaining cusps. The appearance of a metaconid in the fossil specimen can give conclusive evidence about the identity of the specimen: the metaconid is always well individualized in *Canis*, but can be weak and small in *Cuon alpinus*. A weak metaconid is thus a strong indication for a *Cuon alpinus* identity, but a well individualized metaconid was also observed *Cuon alpinus* specimens. Although this occurs much less in *Cuon alpinus* than in *Canis*, a fossil specimen in which the protoconid is not centered and with a well individualized metaconid can still be either *Canis* or *Cuon alpinus* and the identity of the fossil specimen must be determined based on the appearance of the hypo- and entoconid. The hypoconid is always well individualized in *Canis*, but flat and not well individualized in 92% of the *Cuon alpinus* specimens. A not well-discernable hypoconid is thus a strong indication that a specimen is *Cuon alpinus*. On the other hand, a well individualized hypoconid was also observed in *Cuon alpinus* (8% of the specimens). Thus, although this appearance of the hypoconid is rare in *Cuon alpinus*, the presence of a well individualized hypoconid does not entirely exclude *Cuon alpinus* as possibility. The last cusp (entoconid) was absent in most *Cuon alpinus* specimens, but always present in *Canis*. The absence of an entoconid in a fossil specimen is thus a strong indication for a *Cuon alpinus* identity. But also for this cusp the opposite (the presence of a cingular entoconid) is not conclusive evidence for a *Canis* identity, because this was also observed in *Cuon alpinus* (although rarely). A specimen with a well individualized proto-, para- and hypoconid and a cingular entoconid could theoretically thus still belong to *Cuon alpinus*, because the individual appearances of these cusps all were observed in this genus. But the combination of these four principal cusps with a typical *Canis* appearance was never observed in *Cuon alpinus* specimens: in all *Cuon alpinus* specimens of this comparative dataset one or more cusps were absent or had a typical *Cuon alpinus* look. This means that all *Cuon alpinus* specimens could be distinguished from *Canis* solely based on the cusps of their M<sub>2</sub>. We can thus reasonably assume that a specimen with a well individualized proto-, para- and hypoconid and a cingular entoconid is *Canis* and that when one or more of these cusps is absent, not well individualized and/or not positioned in a quadrant the specimen is *Cuon alpinus*.

#### **5.5.4.2b Fossil North Sea material**

For all results that are discussed below see 4.4.5.2b and plate 4.2.

##### **Specimens 534, 535, 667, 1683, 2104, 2620 and 3293**

These seven fossil North Sea specimens all have the typical *Canis* M<sub>2</sub>: a clearly discernable and well individualized proto-, meta- and hypoconid is situated in the mesiobuccal, mesiolingual and distobuccal quadrant respectively and a talonid basin with entoconid-like cingulum occupies the fourth (distolingual) quadrant. All principal cusps are thus present and have the typical *Canis* appearance. This means that these fossil North Sea specimens can be assigned to *Canis* and are certainly not *Cuon alpinus*.

##### **Specimen 2196**

The M<sub>2</sub> of specimen 2196 has typical features of both *Canis* and *Cuon alpinus*. The overall appearance of the tooth is *Canis*-like: the tooth is quite large and broad compared to the second molars of *Cuon alpinus*. Lingually of the hypoconid a small talonid-basin-like depression (bordered by a cingulum) is present, which is never observed in *Cuon alpinus*. These are all indications that specimen 2196 is *Canis*. But the well individualized protoconid is centered in the trigonid, which was never observed in *Canis* specimens. This is an indication that 2196 is *Cuon alpinus*. The well individualized hypoconid is present on the buccal side of the talonid and not centered as in most *Cuons*, although this position was also encountered in *Cuon alpinus*. Thus based on this cusp specimen 2196 still could be either *Canis* or *Cuon alpinus*. Evidence for a *Canis* or *Cuon alpinus* identity is thus equally solid and contradictory. Solely based on the cusps of M<sub>2</sub> specimen 2196 cannot be identified. The cusps of M<sub>1</sub> and the dental formula of 2196 indicated that this specimen cannot be *Cuon alpinus*. This can also be seen from the general size of this hemimandible: it is much too large to be *Cuon alpinus*. We can thus conclude that 2196 has to be *Canis* and that a well individualized protoconid that is centered in the trigonid is also (although rarely) possible in *Canis* specimens.

### 5.5.5 Conclusions section ‘Teeth’

In this paragraph conclusions about the identity of the 13 fossil North Sea specimens will be drawn, based on the combined conclusions of the individual parameters that were presented in this last ‘Teeth’ section. For an overview of all results and interpretation thereof, see appendix XII.

#### **Specimen 534** (*C. l. lupus*)

Specimen 534 was only measured for 4 of the 9 subparameters of the ‘Teeth’ section (Dental formula, length and breadth of  $M_2$  and the cusps of the molars, see table XII.1). The length and breadth of  $M_2$  both confirmed with a 97.7% confidence interval that specimen 534 is not *Cuon alpinus* or *C. l. familiaris*. The conclusion that 534 is not *Cuon alpinus* was extra confirmed by the extended dataset of the breadth of  $M_2$  that included 16 *Cuon alpinus* values from literature. Moreover, based on the dental formula and the cusps of the second molar we concluded with absolute certainty (100% confidence, based on this particular comparative dataset) that specimen 534 is not *Cuon alpinus*, but *Canis*. Based on all combined evidence of this section we can thus conclude with a 97.7% confidence interval that specimen 534 is *C. l. lupus* and not *C. l. familiaris*, and with absolute certainty that 534 is not *Cuon alpinus*, which confirms the conclusions of the previous three sections.

#### **Specimen 535** (*C. l. lupus*)

This fossil North Sea specimen was measured for all parameters in the ‘Teeth’ section, except the ‘Height of the crown’ of  $P_4$  (table XII.1). The dental formula and the cusps of the molars excluded *Cuon alpinus* as possible identity for specimen 535 with absolute certainty. All remaining parameters (Height of the crown of  $M_1$ , Length and breadth of  $M_1$  and  $M_2$ ) excluded with a 97.7% confidence interval both *Cuon alpinus* and *C. l. familiaris*. The conclusion that 535 is not *Cuon alpinus* was extra confirmed by the extended datasets of the length of  $M_1$ , breadth of  $M_1$  and breadth of  $M_2$  that included respectively 28, 23 and 16 *Cuon alpinus* values from literature. Based on all combined evidence of this section we can conclude with a 97.7% confidence interval that specimen 535 belongs to *C. l. lupus*, which reinforces the conclusion of the first section.

#### **Specimen 667** (*C. l. familiaris*)

Specimen 667 was measured for all parameters in the ‘Teeth’ section (table XII.2). Based on the length of  $M_2$  *Cuon alpinus* could be excluded as possible identity for specimen 667 with a confidence interval of 97.7% and the dental formula and the cusps of the molars excluded *Cuon alpinus* with absolute certainty. A *C. l. lupus* identity was excluded with a 97.7% confidence interval by the length and breadth of  $M_1$  and the breadth of  $M_2$ . The possibility of a *C. l. familiaris* identity for 667 was left open by all subparameters. Based on the combined evidence of the ‘Teeth’ section specimen 667 can be assigned to *C. l. familiaris* with a 97.7% confidence interval, which confirms the conclusions of the previous sections.

#### **Specimen 1683** (*C. l. lupus*)

This specimen was also measured for all parameters in the ‘Teeth’ section (table XII.2). All 9 subparameters exclude *Cuon alpinus* as possible identity for specimen 1683, which includes the dental formula and the cusps of the molars that exclude this species with absolute certainty. The results of the extended datasets of the length of  $M_1$ , breadth of  $M_1$  and breadth of  $M_2$  that included respectively 28, 23 and 16 *Cuon alpinus* values from literature confirmed with a 97.7% confidence interval that 1683 is not *Cuon alpinus*. A *C. l. familiaris* identity was excluded by 5 quantitative parameters (Height of the crown of  $P_4$  and  $M_1$ , length and breadth of  $M_1$  and  $M_2$  and breadth of  $M_2$ ), thus the chance that 1683 belongs to this subspecies is even slightly smaller than 2.3%. All subparameters in this section left open the possibility that 1683 is *C. l. lupus* and some subparameters indicated that 1683 is even quite large for a *C. l. lupus* specimen. Based on all combined evidence in this section specimen 1683 can thus be assigned with a 97.7% confidence interval to *C. l. lupus*, which confirms the conclusions of the previous sections.

#### **Specimen 2103** (*C. l. familiaris*)

Specimen 2103 was only measured for 6 subparameters in the ‘Teeth’ section (table XII.3). Two parameters (the dental formula and the cusps of  $M_1$ ) excluded *Cuon alpinus* as possible identity for 2103 with absolute certainty. *C. l. lupus* was only excluded by one parameter (breadth of  $M_1$ ) with a 97.7% confidence interval. Based on the three remaining subparameters specimen 2103 could not be identified. The combination of all evidence in this section points towards a *C. l. familiaris* identity for specimen 2103 with a 97.7% confidence interval, which confirms the conclusions of the previous sections.

#### **Specimen 2104** (*C. l. familiaris*)

This specimen was measured for 7 subparameters in the ‘Teeth’ section (table XII.3). The dental formula and cusps of the molars excluded *Cuon alpinus* with absolute certainty as possible identity for specimen 2104 and a *C. l. lupus* identity was excluded with a 97.7% confidence interval by two quantitative parameters

(length of  $M_1$  and breadth of  $M_2$ ). All other subparameters were inconclusive and all subparameters left open the possibility that 2104 is *C. I. familiaris*. The combined evidence of the 'Teeth' section thus confirms the conclusion of the previous sections that specimen 2104 can be assigned to *C. I. familiaris* with a 97.7% confidence interval.

#### **Specimen 2196 (*C. I. lupus*)**

Specimen 2196 was measured for all parameters of the 'Teeth' section, except the cusps of  $M_2$  (table XII.4). All 9 subparameters exclude *Cuon alpinus* as possible identity for specimen 2196, which includes the dental formula and the cusps of  $M_1$  that exclude this species with absolute certainty. The results of the extended datasets of the length of  $M_1$ , breadth of  $M_1$  and breadth of  $M_2$  that included respectively 28, 23 and 16 *Cuon alpinus* values from literature confirmed with a 97.7% confidence interval that 1683 is not *Cuon alpinus*. The height of the crown of  $P_4$  and  $M_1$  and the length and breadth of  $M_1$  and  $M_2$  excluded *C. I. familiaris* as possibility with a 97.7% confidence interval. The combined evidence of this section indicates that specimen 2196 is a *C. I. lupus* specimen, which confirms the conclusions of the previous sections.

#### **Specimen 2329 (*C. I. lupus*)**

Specimen 2329 was measured for all parameters in this section, except the dimensions of  $M_2$  (table XII.4). Based on all parameters except the breadth of  $M_1$  *Cuon alpinus* was excluded as possibility (with absolute certainty, due to the dental formula and the cusps of  $M_1$ ). A *C. I. familiaris* identity was excluded as possibility for 2329 by the height of the crown of  $P_4$  and  $M_1$  and the length of  $M_1$  (with a 97.7% confidence interval). The combined evidence in the 'Teeth' section indicates with a 97.7% confidence interval that specimen 2329 belongs to the *C. I. lupus* subspecies, which confirms the conclusions obtained in the previous sections.

#### **Specimen 2620 (*C. I. lupus*)**

This fossil North Sea specimen was measured for 7 of the 9 subparameters in the 'Teeth' section (table XII.5). The lengths and breadths of the two molars indicated with a 97.7% confidence interval that specimen 2620 is neither *C. I. familiaris* nor *Cuon alpinus*. The conclusion that specimen 2620 is *Cuon alpinus* was further invalidated by the extended datasets of the length of  $M_1$ , breadth of  $M_1$  and breadth of  $M_2$  that included respectively 28, 23 and 16 *Cuon alpinus* values from literature and by the dental formula and the cusps of the molars (with absolute certainty). A *C. I. lupus* identity was left open as possibility by all subparameters, except the length of  $M_2$  that indicated that this fossil specimen is quite large for a *C. I. lupus* specimen. The combined evidence of the 'Teeth' section indicates with a 97.7% confidence interval that specimen 2620 can be assigned to *C. I. lupus*, which confirms conclusions obtained in previous sections.

#### **Specimen 3219 (*Canis*)**

Specimen 3219 was measured for 6 subparameters in the 'Teeth' section (table XII.5). A *Cuon alpinus* identity was excluded with a 97.7% confidence interval by the height of the crown of  $M_1$  (although the value of 3219 for this parameter was estimated). The cusps of  $M_1$  confirm this, based on which *Cuon alpinus* could be excluded with absolute certainty. The height of the crown of  $M_1$  indicated with a 97.7% confidence interval that specimen 3219 is not *C. I. familiaris*, but the breadth of  $M_1$  indicated with a 97.7% confidence interval that 3219 is not *C. I. lupus*. All remaining subparameters were inconclusive. The subparameters in this section thus confirm the conclusion of the previous sections that specimen 3219 is not *Cuon alpinus*, but still do not provide clear evidence on subspecies level of the identity of specimen 3219, because the only two subparameters that provide a conclusion with a statistical confidence interval contradict each other. Based on the combined evidence of this section the identity of specimen 3219 can only be determined on genus level; it remains unclear whether 3219 should be assigned to *C. I. familiaris* or *C. I. lupus*. This problematic specimen will be discussed further in 5.6.

#### **Specimen 3293 (*C. I. lupus*)**

This specimen was measured for all parameters in the 'Teeth' section (table XII.6). All parameters excluded *Cuon alpinus* as possible identity for specimen 3293 (with absolute certainty based on the dental formula and the cusps of the two molars). These results were confirmed by the extended datasets of the length of  $M_1$ , breadth of  $M_1$  and breadth of  $M_2$  that included respectively 28, 23 and 16 *Cuon alpinus* values from literature. A *C. I. familiaris* identity was excluded by 5 quantitative subparameters (height of the crown of  $P_4$  and  $M_1$ , length of  $M_1$  and  $M_2$  and breadth of  $M_1$ ), which reduces the chance that 3293 is *C. I. familiaris* to less than 2.3%. No 'problems' were encountered for *C. I. lupus*. Based on the combined evidence in the 'Teeth' section we can assign fossil North Sea specimen 3293 to *C. I. lupus* with a 97.7% confidence interval, which confirms conclusions obtained in previous sections.



**Specimen NMR89 (*Canis*)**

Specimen NMR89 was measured for only one parameter in the 'Teeth' section: the dental formula (table XII.6), but this parameter could only identify NMR89 on genus level as belonging to *Canis* and not *Cuon alpinus* (with absolute certainty). This conclusion is consistent with the previous sections, but it remains unclear whether NMR89 should be assigned to *C. l. familiaris* or *C. l. lupus*, because the conclusions of the first two sections were contradictory. This second problematic specimen will be discussed further in 5.6.

**Specimen NMR90 (*Canis*)**

Specimen NMR90 was measured for 6 of the 9 subparameters in the 'Teeth' section (table XII.7). The 'Cusps of the  $M_1$ ' was the only subparameter in this section that indicated that NMR90 is very probably not *Cuon alpinus*, but this evidence is not entirely conclusive, since the conclusion is based on an interpretation of dental features that are present on the  $M_1$  and not the actual presence and direct observation of these cusps. All subparameters left open the possibility that NMR90 is *C. l. familiaris* and a *C. l. lupus* identity was excluded by the length and breadth of  $M_1$  (with a 97.7% confidence interval) and the dental formula (with absolute certainty). Based on the combined evidence of this section (but without a 97.7% confidence interval) can thus be concluded that NMR90 is very probably a *C. l. familiaris* specimen. This confirms the conclusions of the previous section in which NMR90 was identified as *C. l. familiaris* with a 97.7% confidence interval.

We now can combine all conclusions of the individual sections and come to a general and final conclusion on the identity of the 13 fossil North Sea specimens in the final paragraph of this chapter.

## 5.6 General conclusions

The morphological and osteometrical analysis of the 100 Canidae specimens started with 21 parameters that were measured on each specimen, but only 19 parameters proved to be useful for the identification of the 13 fossil North Sea specimens. Moreover, most fossil North Sea specimens could not be measured for all 19 parameters (appendix XII), because all fossil North Sea specimens are eroded to some extent. In addition, we observed that many parameters resulted in ambiguous statements about the identity of the fossil hemimandibles, due to natural variation and a continuum in the characteristics of the comparative (sub)species. All 19 parameters were thus really needed to identify the fossil North Sea specimens with some degree of certainty. For 11 fossil hemimandibles the combined conclusions of the 4 sections were clear and pointed towards the same identity, but even with 19 parameters the results of 2 specimens (3219 and NMR89) were still ambiguous.

Below a brief summary of the conclusions of all 19 parameters is given for each of the 13 fossil North Sea specimens. For each specimen the total amount of subparameters that excluded *C. l. lupus*, *C. l. familiaris* or *Cuon alpinus* with a 97.7% confidence interval or with entire certainty is given of all subparameters that could be measured for that specimen (this does thus not even include any possible strong qualitative evidence). Problematic specimens 3219 and NMR89 are discussed into some more detail. As explained in Chapter 2 and appendix VI, the more parameters with a statistical confidence interval of 97.7% that exclude a (sub)species, the stronger the evidence that the fossil specimen does not belong to that (sub)species (the chance is reduced to less than 2.3%). In table 5.1 below an overview is given for each fossil North Sea specimen of all subconclusions of the four individual sections and the final conclusion on its identity that takes into account all evidence and interpretations as presented in Chapters 3, 4 and 5 (see also appendix XII).

Keeping in mind all assumptions and critical remarks presented in 5.1, assuming that the sample sizes of the comparative *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* material were sufficiently large and assuming that the sizes of the parameters used in this study are normally distributed in the *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* populations, we conclude the following with a 97.7% confidence interval:

### **Specimen 534**

All subparameters left open the possibility of a *C. l. lupus* identity, 6 of the 11 subparameters that were measured excluded *C. l. familiaris* and 9 of the 11 subparameters that were measured excluded *Cuon alpinus* (appendix XII). Specimen 534 is identified as *C. l. lupus*.

### **Specimen 535**

All subparameters left open the possibility of a *C. l. lupus* identity, 6/15 subparameters excluded *C. l. familiaris* and 13/15 subparameters excluded *Cuon alpinus* (appendix XII). Specimen 534 is identified as *C. l. lupus*.

### **Specimen 667**

10/32 subparameters excluded *C. l. lupus*, all subparameters left open the possibility of a *C. l. familiaris* identity and 8/32 subparameters excluded *Cuon alpinus* (appendix XII). Specimen 667 is identified as *C. l. familiaris*.

### **Specimen 1683**

All subparameters left open the possibility of a *C. l. lupus* identity, 18/28 subparameters excluded *C. l. familiaris* and 24/28 subparameters excluded *Cuon alpinus*. Specimen 1683 is identified as *C. l. lupus*.

### **Specimen 2103**

3/29 subparameters excluded *C. l. lupus*, all subparameters left open the possibility of a *C. l. familiaris* identity and 9/29 subparameters excluded *Cuon alpinus* (appendix XII). Specimen 2103 is identified as *C. l. familiaris*.

### **Specimen 2104**

6/31 subparameters excluded *C. l. lupus*, all subparameters left open the possibility of a *C. l. familiaris* identity and 7/31 subparameters excluded *Cuon alpinus* (appendix XII). Specimen 2104 is identified as *C. l. familiaris*.

**Specimen 2196**

All subparameters left open the possibility of a *C. l. lupus* identity, 21/29 subparameters excluded *C. l. familiaris* and 24/29 subparameters excluded *Cuon alpinus* (appendix XII). Specimen 2196 is identified as *C. l. lupus*.

**Specimen 2329**

All subparameters left open the possibility of a *C. l. lupus* identity, 12/30 subparameters excluded *C. l. familiaris* and 21/30 subparameters excluded *Cuon alpinus* (appendix XII). Specimen 2329 is identified as *C. l. lupus*.

**Specimen 2620**

1/24 subparameters excluded *C. l. lupus*, 12/24 subparameters excluded *C. l. familiaris* and 18/24 subparameters excluded *Cuon alpinus* (appendix XII). Although *C. l. lupus* is also excluded as possibility for this specimen, compared to all other evidence that clearly points towards a *C. l. lupus* identity this is insignificant: specimen 2620 is identified as *C. l. lupus*.

**Specimen 3219**

*Cuon alpinus* is excluded as possibility by 10/24 subparameters (appendix XII), which reduces the chance that 3219 is this species to less than 2.3%. Specimen 3219 is thus not *Cuon alpinus*, but the parameters are inconclusive about which *Canis* subspecies 3219 is. Based on almost all parameters both subspecies are possible, and where subparameters are more conclusive, they are contradictory ('Height of the crown'  $M_1$  and breadth  $M_1$ , appendix XII). The parameter 'Height of the crown' for  $M_1$  is the only subparameter that gives a 'problem' in the *C. l. familiaris* column of table XII.5 (red characters). In the *C. l. lupus* column of this table more 'problems' are encountered, but most of these are partial overlaps that do not really reduce the chance that 3219 is *C. l. lupus* and only indicate that 3219 is quite small for a *C. l. lupus* specimen. The only evidence for a *C. l. familiaris* identity that is less ambiguous than the sample and population ranges of the 19 parameters comes from the qualitative comparison of 3219 with the comparative datasets that indicated that 3219 does not compare well to *C. l. lupus* qua overall appearance and looks more fragile like *C. l. familiaris*. This evidence is however far from solid and it can only be guessed that 3219 is possibly a *C. l. familiaris* specimen. Specimen 3219 should be measured for more parameters or undergo a DNA test to be able to make a conclusive statement about its identity.

**Specimen 3293**

All subparameters left open the possibility of a *C. l. lupus* identity, 10/27 subparameters excluded *C. l. familiaris* and 22/27 subparameters excluded *Cuon alpinus* (appendix XII). Specimen 2329 is identified as *C. l. lupus*.

**Specimen NMR89**

*Cuon alpinus* is excluded by 7/17 parameters (appendix XII), thus it can be concluded that NMR89 is not *Cuon alpinus* with a 97.7% confidence interval. Evidence for both *Canis* subspecies is less conclusive, but points slightly towards a *C. l. lupus* identity, because there are three subparameters that indicate that NMR89 is too large for a *C. l. familiaris* specimen and only two subparameters that indicate that NMR89 is too small for a *C. l. lupus* specimen. But when one takes a closer look at the subparameters, we see that the 3 subparameters that indicate that NMR89 is too large for a *C. l. familiaris* specimen are alveolar lengths. These parameters are from the 'Mandible length' section and are indicative of mandible length, while the actual mandible lengths (*a-b* and *c-b*) indicate that NMR89 falls well within the *C. l. familiaris* range. The alveolar lengths of NMR89 thus fit within an average sized *C. l. familiaris* mandible. The mandible height on the other hand, which indicated that NMR89 is too small for a *C. l. lupus* specimen is a more individual parameter. The results of the alveolar lengths and the mandible height are also reflected in the parameter 'Mandible ratios', which indicated that NMR89 has the length of an average *C. l. lupus* specimen, but reduced mandible heights and width like *C. l. familiaris*. From this point of view one could conclude that NMR89 possibly is *C. l. familiaris*. On the other hand the qualitative comparison of NMR89 with *C. l. familiaris* and *C. l. lupus* material indicated that NMR89 looks very similar to a certain comparative *C. l. lupus* specimen with respect to mandible length, width, height and ratios. But qualitatively it was hard to tell whether NMR89 is more similar to *C. l. lupus* or *C. l. familiaris*, because the hemimandible is not extremely thick and robust as typical *C. l. lupus* specimens, but neither clearly thinner and more fragile like typical *C. l. familiaris* specimens. Evidence for the identity of specimen NMR89 is thus vague, ambiguous and contradictory. It is impossible to make any statement of value about the identity of NMR89 on subspecies level. This specimen should also be measured for more parameters and/or undergo a DNA test to be able to make a conclusive statement about its identity.

## Specimen NMR90

This fossil specimen was the specimen of interest, because it was suspected to be *Cuon alpinus*, probably partially due to its dental formula, which indeed indicates that NMR90 is more likely *Cuon alpinus* than *C. l. familiaris* (although last mentioned subspecies cannot be excluded). The dental formula was the only parameter that pointed towards a *Cuon alpinus* identity for NMR90. 4/15 Subparameters excluded *Cuon alpinus* as possibility, all subparameters left open the possibility of a *C. l. familiaris* identity and 5/15 subparameters excluded *C. l. lupus* (appendix XII). A *Cuon alpinus* identity was furthermore excluded by 3 qualitative parameters (the anterior border of the coronoid process, the angular process and the cusps of M<sub>1</sub>). Although evidence is not abundant for this specimen, there are sufficient indicators that NMR90 is not *Cuon alpinus* or *C. l. lupus* (with a 97.7% confidence interval). According to Dick Mol (pers. comm.) NMR90 is an 'extremely small jaw' and he probably partially therefore suspected that NMR90 most probably belongs to neither wolf nor dog, but that of course depends on which species you compare the specimen to. Based on the values of NMR90 for all parameters we can conclude that this specimen is indeed quite/too small compared to *C. l. lupus* and quite/too large compared to *Cuon alpinus* specimens, but average sized compared to *C. l. familiaris*. Since NMR90 is assigned to *C. l. familiaris*, we can conclude that this mandible is not extremely small (it also fell perfectly well within the fossil part of the *C. l. familiaris* ranges of all parameters). NMR90 is thus not a *Cuon alpinus* specimen, as was hypothesized by Dick Mol.

**Table 5.1: Summary of all conclusions on the identity of the 13 fossil North Sea specimens.** For each fossil North Sea specimen the conclusion on its identity per section is given. The last column summarizes the conclusions of the 4 sections and gives the final conclusion on the identity of each fossil North Sea specimen that takes into account all evidence and interpretations as presented in Chapters 3, 4 and 5. See also appendix XII for a summary of all results and interpretations thereof.

Specimen	Section				Specimen identified as
	Mandible length	Mandible W, H, ratios	Ramus	Teeth	
534	<i>C. l. lupus</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>
535	<i>C. l. lupus</i>	<i>Canis</i>	<i>Canis</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>
667	<i>C. l. familiaris</i>	<i>C. l. familiaris</i>	<i>Canis</i>	<i>C. l. familiaris</i>	<i>C. l. familiaris</i>
1683	<i>C. l. lupus</i>	<i>C. l. lupus</i>	<i>Canis</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>
2103	<i>C. l. familiaris</i>	<i>Canis</i>	<i>Canis</i>	<i>C. l. familiaris</i>	<i>C. l. familiaris</i>
2104	<i>C. l. familiaris</i>	<i>Canis</i>	<i>Canis</i>	<i>C. l. familiaris</i>	<i>C. l. familiaris</i>
2196	<i>C. l. lupus</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>
2329	<i>C. l. lupus</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>
2620	<i>C. l. lupus</i>	<i>C. l. lupus</i>	<i>Canis</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>
3219	<i>Canis</i>	<i>Canis</i>	<i>Canis</i>	<i>Canis</i>	<i>C. l. familiaris?</i>
3293	<i>C. l. lupus</i>	<i>Canis</i>	<i>Canis</i>	<i>C. l. lupus</i>	<i>C. l. lupus</i>
NMR89	<i>C. l. lupus</i>	<i>C. l. familiaris</i>	<i>Canis</i>	<i>Canis</i>	<i>Canis</i>
NMR90	<i>C. l. familiaris</i>	<i>Cuon or Canis</i>	<i>Canis</i>	<i>C. l. familiaris</i>	<i>C. l. familiaris</i>

## 6 Final conclusions

The thirteen Canidae hemimandibles from the North Sea were morphologically and osteometrically studied to conclude whether *Cuon alpinus* was a member of the Mammoth Steppe Fauna (the carnivore guild of Northwestern Europe during the Pleistocene). First of all it was verified that the 13 fossil North Sea specimens indeed belong to the Canidae, do not belong to the genus *Vulpes* (foxes) and that the comparative dataset should exist of *Canis lupus lupus* (Eurasian wolf), *Canis lupus familiaris* (domestic dog) or *Cuon alpinus* (dhole) specimens (Chapter 3).

With the identity of the 13 fossil North Sea specimens and the comparative dataset established so far, the two main hypotheses of this thesis could be tested:

- The thirteen fossil hemimandibles from the North Sea are either *Canis lupus lupus*, *Canis lupus familiaris* or *Cuon alpinus*. (According Jelle Reumer pers. comm.)
- Specimen NMR90 is a *Cuon alpinus* specimen. (According to Dick Mol, pers. comm.)

To test these two hypotheses 100 Canidae specimens (the 13 fossil North Sea specimens, 18 comparative *C. l. lupus* specimens, 42 comparative *C. l. familiaris* specimens and 27 comparative *Cuon alpinus* specimens) were measured for 21 morphological and osteometrical parameters (Chapter 4). We observed that two of these parameters (the coronoid angle and the cusps of the premolars) were not indicative of the identity of the fossil North Sea specimens, thus only 19 parameters were eventually used. However, many fossil North Sea specimens could not be measured for all 19 parameters (as depicted in appendix XII), because all fossil North Sea specimens are eroded to some extent. In addition, we observed that many parameters resulted in ambiguous or contradictory statements about the identity of the fossil hemimandibles, due to nature's variation and continuum: there is no distinct separation between species and classification based on supposed typical characteristics is often less reliable and simple as it would seem (exemplified by comparative *C. l. familiaris* specimens 32044 and 74506 that had a typical *Cuon alpinus* dental formula, appendix XIII). All 19 parameters were thus really needed to identify the fossil North Sea specimens with some degree of certainty (Chapter 5).

The most important assumptions that were made in the comparative morphological and osteometrical study and were validated are:

- The sample sizes of the comparative *C. l. lupus*, *C. l. familiaris* and *Cuon alpinus* datasets are sufficiently large (meaning that the comparative dataset is representative for the *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* populations that lived in Northwestern Europe during the Pleistocene with respect to subspecies, locality, age and sex);
- The sizes of the parameters used in this study are normally distributed in the *Cuon alpinus*, *C. l. lupus* and *C. l. familiaris* populations.

The identity of the fossil North Sea specimens could be established with a 97.7% confidence interval based on these two main assumptions (also keeping in mind all other assumptions and critical remarks mentioned in 5.1).

The 13 fossil North Sea specimens were identified as follows: 534: *C. l. lupus*; 535: *C. l. lupus*; 667: *C. l. familiaris*; 1683: *C. l. lupus*; 2103: *C. l. familiaris*; 2104: *C. l. familiaris*; 2196: *C. l. lupus*; 2329: *C. l. lupus*; 2620: *C. l. lupus*; 3219: *C. l. familiaris*?; 3293: *C. l. lupus*; NMR89: *Canis*; NMR90: *C. l. familiaris* (table 5.1). This study showed that in nature there is no nice distinct separation between species as we would like to think. There is much overlap between the size ranges of the comparative material and the fossil specimens often fell within the size ranges of more than one comparative (sub)species. Based on the 19 parameters of this study only 11 of the 13 fossil North Sea specimens could be identified with a sufficient amount of certainty. For specimen 3219 the evidence for a *C. l. familiaris* identity was very sparse and the evidence for specimen NMR89 was thus ambiguous and contradictory that it was impossible to make any statement of value about the identity of NMR89 on subspecies level. Although the identity of these two fossil North Sea specimens could not be established with certainty, the specimen of particular interest (NMR90) could. We can thus confirm the first hypothesis and refute the second:

- Some of the thirteen fossil hemimandibles from the North Sea are indeed *Canis lupus lupus*, others *Canis lupus familiaris*.
- Specimen NMR90 is not a *Cuon alpinus* specimen.

This study does not confirm the presence of *Cuon alpinus* in Northwestern Europe during the Pleistocene. Up to the present moment there is no evidence that *Cuon alpinus* was a member of the Mammoth Steppe Fauna.



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